Dynamics of phytoplankton and heterotrophic bacterioplankton in the western tropical South Pacific Ocean: links with diazotrophic and photosynthetic activity

France Van Wambeke [1], Audrey Gimenez[1], Solange Duhamel[2], Cécile Dupouy[1,3], Dominique Lefevre [1], Mireille Pujo-Pay[4], Thierry Moutin [1]

[1] Aix-Marseille Université, CNRS, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, 13288, Marseille, France
[2] Lamont-Doherty Earth Observatory, Division of Biology and Paleo Environment, Columbia University, PO Box 1000, 61 Route 9W, Palisades, New York 10964, USA
[3] Aix Marseille Université, CNRS, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, 98848, Nouméa, New Caledonia
[4] CNRS, Laboratoire d'Océanographie Microbienne (LOMIC), Sorbonne Universités, UPMC Univ Paris 6, Observatoire Océanologique, 66650, Banyuls/mer

Correspondance to: France Van Wambeke (france.van-wambeke@mio.osupytheas.fr)

Abstract. Heterotrophic prokaryotic production (BP) was studied in the Western Tropical South Pacific using the leucine technique, revealing spatial and temporal variability within the region. Integrated over the euphotic zone, BP ranged 58–120 mg C m^{-2} d^{-1} within the Melanesian Archipelago, and 31–50 mg C m^{-2} d^{-1} within the western subtropical gyre. The collapse of a bloom was followed during 6 days in the south of Vanuatu Islands using a Lagrangian sampling strategy. During this period, rapid evolution was observed in the three main parameters influencing the metabolic state: BP, primary production (PP) and bacterial growth efficiency. With N_2 fixation being one of the most important fluxes fueling new production, we explored relationships between BP, PP and N_2 fixation rates over the WTSP. The contribution of N_2 fixation rates to bacterial nitrogen demand ranged from 3 to 81 %. BP variability was better explained by the variability of N_2 fixation rates than by that of PP in surface waters of the Melanesian Archipelago, which were characterized by N depleted layers and low DIP turnover times (T_{DIP} < 100 h). This is consistent with the fact that nitrogen was often one of the main factor controlling BP on short time scale as shown using enrichment experiments, followed by dissolved inorganic phosphate (DIP) near the surface and labile organic carbon deeper in the euphotic zone. BP variability was better explained by the variability of N_2 fixation rates than by that of PP in surface waters of the Melanesian Archipelago, which were characterized by N depleted layers, and low DIP turnover times (T_{DIP} < 100 h). However, BP was more significantly correlated with PP but not with N_2 fixation rates where DIP was more available (T_{DIP} > 100 h), deeper than the euphotic zone in the Melanesian Archipelago, or within the entire euphotic zone in the subtropical gyre. The bacterial carbon demand to gross primary production ratio ranged 0.75 to 3.1. These values are discussed in the frame of various assumptions and conversion factors used to estimate this ratio, including the methodological errors, the daily variability of BP, the bacterial growth efficiency and one bias so far not considered; the possibility for *Prochlorococcus* to assimilate leucine in the dark.

1 Introduction

Heterotrophic prokaryotes can process, on average, 50 % of the carbon (C) fixed by photosynthesis in many aquatic systems (Cole, 1988). Understanding the controls of heterotrophic bacterial production and respiration rates is fundamental for two major aspects of marine C cycling: i) to explore the possible fate of primary production through the microbial food web, and ii) to construct a metabolic balance based on C fluxes. To asses these two major features, bacterial carbon demand (BCD, i.e. the sum of heterotrophic bacterial production (BP) and bacterial respiration (BR)) is compared to primary production (PP). The metabolic state of the ocean, and in particular the status of net heterotrophy within oligotrophic

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Supprimé: Bacterial growth efficiency (BGE) ranged from 6 –10 %. Applying correcting factors to estimate gross primary production and correcting BP for *Prochlorococcus* assimilation of leucine, we showed a large variability in the contribution of gross primary production to bacterial C demand. Exploration of a bloom collapse at one site south of Vanuatu showed the importance of blooms, which can persist over extensive distance for long periods of time, and can maintaining net autotrophy where they occur. Using a Lagragian sampling strategy during 6 days, long duration sites allowed for the study of the rapid changes including BP, primary production and BGE, that occurred during the bloom collapse.
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systems, has been largely debated in the last decade (see for example review in Duarte et al., 2013; Ducklow and Doney, 2013; Williams et al., 2013).

The South Pacific gyre (GY) is ultra-oligotrophic, and is characterized by deep UV penetration, by deep chlorophyll maximum (dcm) depth as great as 200 m, and by a 0.1 µM nitrate (NO3) isocline at 160 m (Claustre et al., 2008b; Halm et al., 2012). Our knowledge of the South Pacific Ocean's metabolic state based on C fluxes is fragmentary, since only little primary production data has previously been reported, and never simultaneously with BP (see references in Table 1). The exception is the BIOSOPE cruise conducted in the GY and Eastern tropical south Pacific (ETSP) in Nov./Dec. 2004, where both PP and BP were estimated simultaneously (Van Wambeke et al., 2008b).

The waters coming from the GY are essentially transported by the South Equatorial current toward the Melanesian archipelagos in the Western Tropical South Pacific (WTSP). Interest in this region has increased due to field and satellite observation showing intermittent phytoplankton blooms in the area associated with *Trichodesmium* (Dupouy et al., 1988; 2011; Tenorio et al., 2018). The WTSP is a highly dynamic region (Rousselet et al., 2017) where patches of chlorophyll blooms can persist for up to a few weeks (de Verneil et al., 2017b). The WTSP is a hotspot for biological nitrogen fixation (N_2fix, Bonnet et al., 2017), extending to this whole oceanic region what was already measured near New Caledonia (Garcia et al., 2007). Based on nitrogen budgets, such blooms can sustain significant new production and export in this area (Caffin et al., 2017). The development of these blooms are explained by different hypotheses, including temperature thresholds (in particular regulating *Trichodesmium* blooms); increased light providing more energy; the stratification of surface waters favoring depletion of nitrate and reducing competition with non-fixing primary producers; and increased availability of iron and phosphate (DIP) due to island mass effects, volcanic activities or atmospheric nutrient deposition (Moutin et al., 2005; 2008; Luo et al., 2014; Martino et al., 2014; Shiozaki et al., 2014, Bonnet et al., 2018).

While the dynamics of heterotrophic prokaryotes coupling with primary producers has been explored in many regions of the ocean, these processes have not been studied in the WTSP. Because most oligotrophic oceans are nitrogen limited, PP and N_2fix have already been sampled simultaneously in diverse studies and their relationships examined. Taking a Redfield ratio of 6.6, the contribution of N_2fix rates to PP, integrated over the euphotic zone, has been found to range from 1–9 % in diverse provinces of the Atlantic (Fonsesca et al., 2016). The ratio is 15– 21 % in the WTSP and 3–4 % in the centre of the GY (Raimbault and Garcia, 2008; Caffin et al., 2017). Few studies have attempted to examine how the variability of nitrogen fixation can be linked to that of heterotrophic activity, or to identify the contribution of N_2fix rates to heterotrophic prokaryotic N demand. Yet, recent genomic analyses exploring the diversity of the nitrogenase reductase (*nifH*) gene have revealed the importance of non-cyanobacterial nitrogen fixers (Gradoville et al., 2017 and ref therein). Owing to the fact that a great abundance of *nifH* gene copies does not imply that N_2 fixation is occurring (see for example Turk-Kubo et al., 2014), diverse tests have been conducted to assess heterotrophic N_2 fixation indirectly. For example, in the oligotrophic Eastern Mediterranean Sea, aphotic N_2 fixation can account for 37 to 75 % of the total daily integrated N_2fix rates (Rahav et al., 2013). In the Red Sea, N_2fix rates are correlated to BP but not to PP during the stratified summer season, while during a *Trichodesmium* bloom in winter, both PP and BP increased with N_2fix rates although the correlation was still insignificant with PP (Rahav et al., 2015). In the South Pacific, the presence of non-cyanobacterial nitrogen fixers has been detected in the dark ocean as the in euphotic layer, with detectable levels of *nifH* gene expression, as measured by qPCR or N_2fix activity determined in darkness (in the GY: Halm et al., 2012, Moisander et al., 2014; in the Eastern Tropical South Pacific Ocean: Bonnet et al., 2013, in Bismarck and Solomon Seas: Benavides et al., 2015). The addition of selected organic molecules such as glucose (Dekaezemacker et al., 2013) or natural organic matter such as Transparent Expolymer Particles, can influence N_2fix rates (Benavides et al., 2015). Finally, recent experiments based on incubation with ^{15}N-labeled N_2 coupled to nano-SIMS analyses also demonstrated that a rapid transfer, at the scale of 24 to 48 h, can occur between N_2 fixers, non-fixing phytoplankton and heterotrophic prokaryotes (Bonnet et al., 2016).

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In this study, we examined the horizontal and vertical distribution of heterotrophic prokaryotic production alongside photosynthetic rates, N_2fix rates and phosphate turnover times across the WTSP, in order to relate these fluxes with bottom-up controls (related to nitrogen, phosphate and labile C availability). Particular attention was given to determine the coupling between BP and PP or N_2fix rates, to examine the variability of bacterial carbon demand (BCD) in comparison to gross primary production (GPP) ratios and to discuss the metabolic state of this region

2 Materials and methods

2.1 Sampling strategy

The OUTPACE cruise (doi.org/10.17600/15000900) was conducted in the WTSP region, from February 18th to April 3rd, 2015, along a transect extending from the North of New Caledonia to the western part of the South Pacific Gyre (WGY) (25°S 115 E – 15°S, 149°W, Fig. 1). For details on the strategy of the cruise, see Moutin et al. (2017). Stations of short duration (< 8 h, fifteen stations named SD1 to SD15, Fig. 1) and long duration (6 days, three stations named LDA to LDC) were sampled. Generally, at least 3 CTD casts going down to 200 m were conducted at each short station, except at SD5 and SD9 (two casts) and at SD13 (one cast). The LD stations were abbreviated as LDA (north New Caledonia), LDB (Vanuatu area) and LDC (oligotrophic reference in the WGY area). LD stations were selected using satellite imagery, altimetry and Lagragian diagnostics (Moutin et al; 2017), as well as on the abundance of selected diazotrophs *nifH* gene copies, analyzed by quantitative Polymerase Chain Reaction (qPCR), in real time on board (Stenegren et al. 2018). At these LD stations, CTD casts were performed every 3 hours during at least 5 days. All samples were collected from a CTD-rosette system fitted with 20 12-L Niskin bottles and a Sea-Bird SBE9 CTD.

At the SD stations, water samples used for measuring *in situ*–simulated primary production (PP_{deck}), dissolved inorganic phosphate turnover times (the ratio of DIP concentration to DIP uptake rate, T_{DIP}), N_2fix rates came from the same rosette cast as water used for measuring BP. At the LD sites, we also conducted biodegradation experiments to determine bacterial growth efficiency (BGE), along with enrichment experiment to explore the factors limiting BP. In addition to the measurements of chlorophyll *a*, BP, PP, T_{DIP} and DOC described below, other data presented in this paper include hydrographic properties, nutrients and N_2fix, for which detailed protocols of analysis and considerations for methodology are available in Moutin et al. (2017; 2018) and Bonnet et al. (2018). Briefly, DIP and nitrate concentrations were measured using standard colorimetric procedures on a AA3 AutoAnalyzer (Seal-Analytical). The quantification limits were 0.05 µM for both nutrients. N_2 fixation rates were measured using the $^{15}N_2$ tracer method in 4.5 L polycarbonate bottles inoculated with 5 ml of $^{15}N_2$ gas (99 atom % ^{15}N, Eurisotop). Note that the risk of underestimation by this bubble method was checked by subsampling and fixing 12 ml of each bottle after incubation and to analyze the dissolved $^{15}N_2$ with a Membrane Inlet Mass Spectrometer.

2.2 Chlorophyll a

For chlorophyll a (chl a), a sample of 288 mL of seawater was filtered through 25 mm Whatman GF/F filters immediately after sampling and placed at -80°C in Nunc tubes until analysis. At the laboratory (3 months after the cruise), after grinding the GF/F filter in 5 ml methanol, pigments (chl a and phaeophytin) were extracted in darkness over a 2 h period at 4°C and analyzed with a Trilogy Turner 7200-000 fluorometer according to Le Bouteiller et al. (1992). Sampling for chl a analysis started only at station LDA (Dupouy et al., 2018). In vivo fluorescence was performed with an AquaTraka III (ChelseaTechnologies Group Ltd) sensor mounted on the CTD.

The overall correlation of in vivo fluorescence (chl iv) with chl a was very patchy (chl a=1.582 * chl iv + 0.0241, n = 169, r = 0.61). This is due to the heterogeneity at the time of sampling and the nature of the populations present, i.e.

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essentially different fluorescence yields over depth and species (Neveux et al., 2010). Thus in vivo fluorescence was used only to track high frequency variability at the LD sites, the shape of vertical profile's distributions and the location of the dcm, as well as longitudinal trends. Fluorometric discrete data (chl a) was for calculating and comparing integrated chl a stocks.

2.3 Bacterial production

Bacterial production (BP, *sensus stricto* referring to heterotrophic prokaryotic production) was determined onboard using the microcentrifuge method with the ^{3}H- leucine (^{3}H-Leu) incorporation technique to measure protein production (Smith and Azam, 1992). Triplicate 1.5 mL samples and a killed control with trichloracetic acid (TCA) at 5 % final concentration were incubated with a mixture of [4,5-^{3}H]leucine (Amersham, specific activity 112 Ci mmol^{-1}) and nonradioactive leucine at final concentrations of 7 and 13 nM, respectively. Samples were incubated in the dark at the respective *in situ* temperatures for 1–4 h. On nine occasions, we checked that the incorporation of leucine was linear with time. Incubations were ended by the addition of TCA to a final concentration of 5 %, followed by three runs of centrifugation at 16000 g for 10 minutes. Bovine serum albumin (BSA, Sigma, 100 mg l^{-1} final concentration) was added before the first centrifugation. After discarding the supernatant, 1.5 ml of 5 % TCA was added before the second centrifugation. For the last run, after discarding the supernatant, 1.5 ml of 80 % ethanol was added. The ethanol supernatant was then discarded and 1.5 ml of liquid scintillation cocktail (Packard Ultimagold MV) was added. The radioactivity incorporated into macromolecules was counted in a Packard LS 1600 Liquid Scintillation Counter on board the ship. A factor of 1.5 kg C mol leucine^{-1} was used to convert the incorporation of leucine to carbon equivalents, assuming no isotopic dilution (Kirchman, 1993). Indeed, isotopic dilution ranged from 1.04 to 1.18 as determined on five experiments where we checked the saturating level of ^{3}H-leucine. Standard deviation associated with the variability between triplicate measurements averaged 12 % and 8 % for BP values lower and higher than 10 ng C l^{-1} h^{-1}, respectively. At the LD sites, BP was sampled every day at 12:00 local time.

2.4 Primary production ant phosphate turnover times

Primary production (PP) and dissolved inorganic phosphate turnover times (T_{DIP}) were determined using a dual ^{14}C–^{33}P labelling technique following Duhamel et al. (2006) and described in Moutin et al. (2018). Briefly, after inoculation with 10 µCi of ^{14}C sodium bicarbonate and 4 µCi of ^{33}P-orthophosphoric acid, 150-mL polycarbonate bottles were incubated in on-deck incubators equipped with blue screens (75, 54, 36, 19, 10, 2.7, 1, 0.3 and 0.1 % incident light, https://outpace.mio.univ-amu.fr/spip.php?article135) and flushed continuously with surface sea water. Incubation times lasted 4 (western stations) to 24 h (South Pacific Gyre area) and were chosen according to expected T_{DIP}. Samples were then filtered through 0.2 µm polycarbonate membranes, with radioactivity retained by the filters being assessed by liquid scintillation counting directly on board and after 12 months in the laboratory. Rates of daily primary production were computed using the conversion factors $\tau_{(Ti\,;T)}$ according to Moutin et al. (1999) to calculate normalized (dawn-to-dawn) daily rates from the hourly rates measured in the on-deck incubators (PP_{deck}).

Measurements of PP using the JGOFs protocol (*in situ* moored lines immerged for 24 h from dawn to dawn, $IPP_{in\ situ}$) were also performed at each long stations on days 1, 3 and 5 (see Caffin et al., 2017 for details). Integrated rates within the euphotic zone were estimated by trapezoidal integrations, assuming the same rate between 0 m and the shallowest layer sampled, and considering PP to be zero at 20 m below the deepest sampled depth.

2.5 Bacterial growth efficiency and dark community respiration

Bacterial growth efficiency (BGE) and DOC lability were estimated at the three LD sites using dilution experiments with seawater sampled in the mixed layer. The seawater used for the experiments was sampled from Niskin bottles (9 m at

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LDA, 7 m at LDB and 16 m at LDC) from a CTD cast done at 12:00 local time on the first day of measurements at each LD site. A 1/5 dilution culture was established by mixing a bacterial inoculum from the same water sample (0.4 L of a < 0.8 µm filtrate) with 1.6 L of < 0.2 µm filtrate, in a borosilicate bottle. We incubated them in the dark, for up to 10 days, in a laboratory incubator set at *in situ* temperature. Periodically, for up to 10 days, subsamples were taken to estimate DOC concentrations and bacterial production. The BGE was estimated from DOC and bacterial production estimates on a given time interval corresponding to the exponential phase of BP following Eq. (1):

$$BGE = BP_{int} / DOC_{cons} \quad \text{(eq 1)}$$

where BP_{int} is the trapezoidal integration of BP with time for the period considered, and DOC_{cons} the dissolved organic carbon consumed during that period, corresponding to the difference in DOC concentration between initial ($DOC_{initial}$) and minimal DOC (DOC_{min}). From these experiments we determined also the labile fraction of DOC (LDOC) was determined following Eq. (2):

$$LDOC = (DOC_{initial} - DOC_{min}) / DOC_{initial} \quad \text{(eq 2)}$$

Samples for dissolved organic carbon were filtered through two precombusted (24h, 450°C) glass fiber filters (Whatman GF/F, 25 mm) using a custom-made all-glass/Teflon filtration syringe system. Samples were collected into precombusted glass ampoules and acidified to pH 2 with phosphoric acid (H_3PO_4). Ampoules were immediately sealed until analyses by high temperature catalytic oxidation (HTCO) on a Shimadzu TOC-L analyzer (Cauwet, 1999). Typical analytical precision is ± 0.1–0.5 (SD) or 0.2–0.5 % (CV). Consensus reference materials (http://www.rsmas.miami.edu/groups/biogeochem/CRM.html) was injected every 12 to 17 samples to insure stable operating conditions.

Rates of dark community respiration (DCR) were used to estimate bacterial growth efficiency (see discussion). Briefly, DCR was estimated from changes in the dissolved oxygen (O_2) concentration during dark incubations of unfiltered seawater (24 h) carried out at LD stations, *in situ* on the same mooring lines used for $PP_{in\ situ}$ (Lefevre et al., this issue). Quadruplicate Biological Oxygen Demand bottles were incubated in the dark at each sampled depth. The concentration of oxygen was determined by Winkler titration. DCR were calculated as the difference between initial and final O_2 concentrations. The mean standard error of volumetric DCR rates was 0.28 µmol O_2 dm^{-3} d^{-1}.

2.6 Enrichment experiment

Enrichments experiments were performed along vertical profiles at the three sites LDA, LDB and LDC. Seawater was sampled at 12:00 PM local time on day 2 of occupation at each site. Nutrients were added in 60 ml transparent polycarbonate bottles at a final concentration of 1 µM NH_4Cl + 1µM $NaNO_3$ in 'N' amended bottles, 0.25 µM Na_2HPO_4 in 'P' amended bottles, 10 µM C-glucose in 'G' amended bottles. The sum of all these elements were added in 'NPG' amended bottles. Controls 'C' were left unamended. Bottles were incubated on average for 24 h under simulated *in situ* conditions (in the same on-deck incubators than those used for PP_{deck}). Selected depths chosen encompassed the euphotic zone. At LDA: 9, 24, 35, 70, 100 m were incubated under 54, 10, 3 1 and 0.3 % incident light; at LDB: 7, 12, 27, 42 m were incubated under 54, 36, 10, and 3 % incident light, and at LDC: 16, 60, 91 and 135 m were incubated under 54, 10, 3, and 1 % incident light, respectively. For depths deeper than the euphotic zone (200 m at LDA, 100 m and 200 m at LDB, and 200 m at LDC), flasks were incubated in the dark in a laboratory incubator set at *in situ* temperature. After 24 h of incubation, subsamples were taken from each flask to perform BP incubations as described for *in situ* samples (triplicate estimates, incubation in the dark), except that incubations lasted only 1 h. Results are presented as enrichment factor relative to the unamended control.

2.7. Statistics

Relationships between variables were established using model II Tessier linear regressions, from log-transformed data. Multiple regressions were also used to study the simultaneous effects of PP and N_2fix rates on BP variability. The

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effect of enrichments was tested comparing BP obtained in the unamended control with BP obtained in the amended samples using a Mann-Whitney non parametric test. . This test was also used to estimate differences between geographic zones described in Table 2. Standard errors (s.e.) of integrated rates were calculated following the propagation procedures.

3. Results

3.1 Regional oceanographic settings

The transect started North West of New Caledonia, crossed the Vanuatu and Fidji Arcs and finished inside the west part of the ultra-oligotrophic South Pacific Gyre (Fig. 1). It covered a vast region of the WTSP and the main gradient of biogeochemical and biological properties between the Melanesian Archipelago (MA) (stations SD1 to SD12 and LDA) and the western part of the South Pacific Gyre (WGY) (SD13 to SD15 and LDC) separated by the Tonga Volcanic Arc (Fig. 1). Temperatures ranged 19.7–30.2°C within the 0–200 m layer (see Fig 3a in Moutin et al., 2017). Density revealed shallow mixed layers, due to the sharp temperature gradients. The transition between these the MA and WGY is particularly evidenced by enhanced degree of oligotrophy in the WGY. The WGY was characterized by dcm depth greater than 115 m (Table 2), a deep nitracline (130 m), nitrite peaks around 150 m and detectable amounts of phosphate at the surface (> 100 nM, Moutin et al., 2018). A detailed analysis of the vertical distribution of nutrients and organic matter made it possible to separate two types of stations within the MA; one group between 160 and 170°E called WMA for 'Western Melanesian Archipelago' clustered SD1, 2, 3 and LDA and a second group South of Fidji called EMA for 'Eastern Melanesian Archipelago' clustered SD6, 7, 9 and 10 (Moutin et al., 2018). Main biogeochemical differences between these two groups of stations were related to shallower depths for phosphacline (20 m), nitracline (76 m), dcm (82 m) in the WMA group (see Table 2 and Figure 5 b, c in Moutin et al., 2018). The EMA group had depths for these parameters intermediate to those recorded at the WMA and WGY groups (phosphacline 44 m, nitracline 100 m and dcm 105 m). Although geographically included within the MA area, LDB corresponded to a particular bloom condition and is therefore presented and discussed separately.

3.2 Longitudinal distributions

The mixed layers for most of the cruise were ≤ 20 m (Moutin et al., 2018, de Verneil et al., 2017a), except at SD13 and LDC where the mixed layer depths were 27 and 34 m respectively. The dcm depth ranged between 61 and 115 m in the MA and between 123 and 154 m in the WGY (Table 2, see Fig 3d in Moutin et al., 2017). Integrated chlorophyll a concentrations ranged from 13 to 23 mg chl a m^{-2} in the WGY, and were significantly lower than in the MA (20–38 mg chl a m^{-2}, Mann-Whitney test, p = 0.013). The mean dcm depth within the EMA was slightly deeper (105 ± 10 m, Table 2) than in the WMA (82 ± 10 m, Mann-Whitney test, p = 0.03).

Maximum primary production rates reached 20.8 mg C m^{-3} d^{-1} (Fig 2a). PP rates greater than 10 mg C m^{-3} d^{-1} were obtained in the MA area at SD1, SD7, and SD9 and also at sites LDA and LDB (see below), whereas stations in the WGY showed values lower than 1.3 mg C m^{-3} d^{-1}. Bacterial production ranged from 0.8 to 138 ng C l^{-1} h^{-1} in the 0–200 m layer (Fig. 2b). Within the MA, BP reached values higher than 100 ng C l^{-1} h^{-1} at SD1 and SD5 within the surface (5 m depth, Fig. 2b). High BP values were also obtained at LDB (see below). Within the WGY, maximum BP rates reached 27 ng C l^{-1} h^{-1} (at site LDC, see below).

Integrated primary production (IPP_{deck}) ranged from 178 to 853 mg C m^{-2} d^{-1} within the MA and from 104–213 mg C m^{-2} d^{-1} within the WGY (Fig. 3a). Integrated BP (IBP) over the euphotic zone ranged from 58 to 120 mg C m^{-2} d^{-1} within the MA and from 31 to 35 mg C m^{-2} d^{-1} within the WGY (Fig. 3a). Both integrated fluxes within the euphotic zone were statistically lower within WGY (Mann-Whitney test, p = 0.01 for IBP, and p = 0.03 for IPP_{deck}). In contrast, for the WMA

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The transect covered a vast region of the WTSP and the main transition in distribution of biogeochemical and biological properties corresponded to sub regions geographically separated by the Tonga volcanic arc: the Melanesian Archipelago (MA) area was covered by stations SD1 to SD12, and included LDA.
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and EMA group of stations, integrated fluxes were not statistically different, neither for IBP (99 ± 15 versus 95 ± 12 mg C m^{-2} d^{-1}, Mann-Whitney test, $p > 0.05$) nor for IPP_{deck} (481 ± 47 versus 471 ± 276 mg C m^{-2} d^{-1}, $p > 0.05$)

DIP turnover times (T_{DIP}) ranged over 4 orders of magnitude along the transect (from 2.1 up to 1000 h, Fig. 4). T_{DIP} roughly increased with depth, coincident with the increase of DIP concentrations below the phosphacline. T_{DIP} also showed a clear MA–WGY transition zone. Within the WGY mixed layers, T_{DIP} ranged from 469–4200 h (Fig. 4a), coincident with detectable amounts of DIP (around 100 nM) in this area (Moutin et al., 2018). T_{DIP} were lower in the MA than in the WGY. However, T_{DIP} ranged from 2–857 h in the mixed layers of the MA, with lower values associated to stations LDB-d5, LDA-d5, SD3, SD4 and SD6, and with elevated values being measured at SD2 SD5, SD7 and SD12. This T_{DIP} range, encompassing two orders of magnitude, suggests a much higher range of DIP avaulability than DIP concentration alone would suggest. Below the phosphacline, T_{DIP} increased with depth more sharply in the WMA (Fig 4a) than for the EMA (Fig. 4b).

3.3 Daily variability at the long occupation sites.

Site LDA showed variable dcm depth during the occupation time, with patches of in vivo fluorescence moving up and down the water column with time over a band of 40 m height (dcm depth varied between 63 and 101 m, Table 2), However, the dcm depth corresponded to a stable density horizon (σt 23.55 ± 0.04 kg m^{-3}), with its fluctuation corresponding to internal waves characterized by a periodicity of about 2 per day (Bouruet-Aubertot et al. this issue; Fig. 5). BP and PP peaked in shallower layers, at 10–25 m depth (range 47–68 ng C l^{-1} h^{-1} for BP, and 3–6 mg C m^{-3} d^{-1} for PP) and sometimes presented a second, much less intense peak, close to the dcm depth (Fig. 5). Overall, BP and PP showed parallel trends, increasing slightly on day 3 compared to days 1 and 5. Integrated chl a was on average 26.0 ± 2.6 mg chl a m^{-2}, $IPP_{in\ situ}$ 267 ± 79 mg C m^{-2} d^{-1} and IBP 98 ± 16 mg C m^{-2} d^{-1} (Table 2). I-DCR means (± sd) were 226 ± 43 mmole O_2 m^{-2} d^{-1} (Table 2).

Site LDB, sampled inside a high chlorophyll patch, showed maxima of in vivo fluorescence between 10 and 77 m, the chlorophyll maximum depth showing a significant linear deepening with time (10.4 ± 0.8 m d^{-1}, $r = 0.89$, $n = 45$, $p < 0.001$). Contrarily to site LDA, the dcm depth did not correspond to a stable pycnocline horizon, as density associated with the dcm depth varied between 21.8 and 23.9 kg m^{-3} and reached a plateau after day 4 (data not shown). Chl was distributed over a larger layer (between the surface and 80 m) during the first three days, and then presented a narrower and deeper zone of accumulation, with intensities increasing (Fig. 6). Integrated chl a decreased from 53.2 to 23.9 mg chl a m^{-2} between days 1 and 5, which corresponded to a chlorophyll biomass net loss of about 7.3 mg chl m^{-2} d^{-1}. The shape of BP and PP vertical profiles was particularly modified at day 5, showing a small decrease of subsurface values for BP (125 down to 100 ng C l^{-1} h^{-1}) but a larger one for PP (15 down to 9 mg C m^{-3} d^{-1}). In contrast, BP increased within the dcm depth at day 5. Integrated PP decreased by approximatively 145 mg C m^{-2} d^{-1} between days 3 and 5. PP was not measured at day 4, but a decrease of BP rates in sub-surface layers was already visible. Six profiles were available for BP from which we estimated a linear increasing trend of 7.2 mg C m^{-2} d^{-1} per day ($n = 6$, $r = 0.78$). I-DCR decreased with time from 185 to 151 mmole O_2 m^{-2} d^{-1}, from day 1 to day 5, respectively.

Site LDC, typical of the ultra-oligotrohic WGY, presented a deeper dcm depth, ranging between 115 and 154 m, due to internal waves (Fig. 7). Similarly to site LDA the dcm depth corresponded to a stable density horizon (σt 24.59 ± 0.02 kg m^{-3}, $n = 46$). PP exhibited two peaks around 40–60 m and 120 m, but remained very low (max 2.3 mg C m^{-3} d^{-1}) compared to the other sites LDA and LDB. BP profiles paralleled those of PP, reaching also small maxima at 60 m and occasionally a second one at 120 m. Maximum BP rate was 27.7 ng C l^{-1} h^{-1}. $IPP_{in\ situ}$ ranged from 149 to 165 mg C m^{-2} d^{-1}, I-DCR ranged from 103 to173 mmole O_2 m^{-2} d^{-1}. IBP values were also low (44 ± 5 mg C m^{-2} d^{-1}) and the three integrated rates exhibited no trend with time.

3.4 Relationships between BP, PP, N_2fix and T_{DIP}

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There are several limitations when comparing PP_{deck} and $PP_{in\ situ}$. Incubation on mooring lines for 24h dawn to dawn is considered to be a good compromise by JGOFS recommendations (JGOFS, 1988), as conditions of temperature and light are close to in situ (except UV). Incubation on deck under simulated *in situ* conditions suffers from biases related to the use of artificial screens to mimic light attenuation with depth and also from biases related to temperature differences for deeper samples, as they are incubated at sea-surface temperature. During our cruise, at each LD site on day 5, we used both incubation methods, but unfortunately did not sample the same ctd cast: $PP_{in\ situ}$ was sampled at 3:00 AM while PP_{deck} was sampled at 9:00 AM. At site LDA, differences between the mean $IPP_{in\ situ}$ and IPP_{deck} were particularly high. Besides artifacts related to screens and temperature described above, this difference could also be due partly to internal waves. For instance at the site LDA on day 5, the dcm depth changed from 69 m to 87 m between the 3:00 AM ctd cast and the 9:00 AM ctd cast. At the site LDB, the bloom collapsed rapidly and a trend with time was clearly detected, making the comparison between both methods impossible, even with only a time lag of 6 h. For this reason, and to keep relative comparisons consistent, we used only PP_{deck} data when exploring relationships between BP, PP, N_2fix and T_{DIP}.

Log-log relationships between BP and PP_{deck} presented similar trends for all samples with T_{DIP} values below or above 100 h (Fig. 8a). Values below 50–100 h are representative of a restricted access to DIP by microorganisms (Moutin et al., 2008). T_{DIP} below 2 days was shown to be critical for *Trichodesmium* spp. growth (Moutin et al., 2005). The depth at which this threshold was reached varied from surface to 64 m in MA although all T_{DIP} values were higher than 100 h in the WGY. For samples where T_{DIP} was ≤ 100 h and > 100 h log-log relationships were, respectively:

log BP=0.842 log PP - 0.57, n=47, r = 0.26, p = 0.04 and

log BP=0.808 log PP - 0.53, n=90, r = 0.67, p < 0.001

In contrast, log-log relationships linking BP and N_2fix presented different trends for samples corresponding to depths where T_{DIP} was below or above 100 h (Fig. 8b). For samples where T_{DIP} was ≤ 100 h and > 100 h, relationships were, respectively:

log BP=0.752 log N_2fix - 0.78, n=39, r = 0.52, p < 0.001, and

log BP=0.438 log N_2fix - 0.31, n=55, r = 0.43, p < 0.001

This shows that BP was more correlated with N_2fix than with PP_{deck} in the surface, P-depleted waters of the MA. However, as PP_{deck} and N_2fix could co-vary, a multiple regression BP = f (PP_{deck}, N_2fix) was tested (Table 3). The partial coefficient was not significant for N_2fix for samples with T_{DIP} > 100 h. The partial coefficients were both significant for N_2fix and for BP for samples characterized by T_{DIP} ≤ 100 h, but N_2fix better explained the distribution of BP in the multiple regression analysis compared to PP (t-test, p=0.024 for PP and p < 0.0001 for N_2fix).

Integrated N_2fix accounted for 3.3 to 81 % of the bacterial nitrogen demand along the transect, assuming a stoichiometric molar C/N ratio of 5 for heterotrophic prokaryotic biomass (Fig. 3b). Among the three LD sites, the variability of this ratio was lower at sites LDA and LDC, with no particular temporal trend at any of these sites. The ratio ranged from 28 to 46 % at LDA, with a mean of 37 % ± 9 %, greater than that obtained at LDC (range 6–10 %, mean ± sd 8 % ± 2 %). The ratio exhibited no particular temporal trend, whereas a decrease was clearly observed at LDB, (68 %, 37 % and 19 % on day 1, 3 and 5, respectively). This was due to a simultaneous decrease of integrated N_2fix rates (from 0.98 ± 0.058 mmole N m^{-2} d^{-1} on day 1, to 0.758 ± 0.058 and 0.38 ± 0.019 mmole N m^{-2} d^{-1} on days 3 and 5, respectively) and an increase of IBP as described in section 3.3, The mean contribution was 40 ± 20 % over all the transect, and including data from LD sites (n = 26 profiles).

We also examined relationships between T_{DIP} and other biological fluxes using multiple regressions [logT_{DIP}=f(log PP, log N_2fix, log BP)], incorporating 91 samples for which the three rates were measured simultaneously (Table 4). The partial coefficients were both significant for both N_2fix (p < 0.0001) and BP (p = 0.003) but not for PP (p = 0.23). As all biological rates decreased with depth, we also examined this correlation using data within the mixed layer to avoid the depth

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effect. With this restricted data set (47 samples) the partial coefficients were significant only for BP ($p = 0.0024$) and just under the significance threshold for N_2fix ($p = 0.056$) and still non-significant for PP.

3.5 DOC lability and BGE

In the three biodegradation experiments starting on day 1 at each LD site using sub-surface waters, BP increased significantly, with growth rates (determined from exponential phase of BP increase) ranging from 0.08 to 014 h^{-1}. DOC was slightly consumed, with DOC concentrations decreasing only 2 to 5 % over 10 days, and with the lowest percentage of labile fraction being measured at site LDC (Table 5). Bacterial growth efficiencies were 13, 6.3 and 6.7 % in sites LDA, LDB and LDC, respectively (Table 5).

3.6 Enrichment experiments

Conditions prevailing before enrichments are presented together with enrichment factors obtained at the different depths tested as vertical distributions of in vivo fluorescence, nutrients and BP sampled from a CTD cast starting at 12:00 PM on day 2 of each LD site (Fig. 9). Nitrate concentrations were below the detection limits of standard methods in upper layers. The depth of the nitracline varied with the dcm depth at LDA and LDC (100 m at LDA, 135 m at station LDC) but not at LDB (a large peak of chlorophyll was observed within 20–70 m with a nitracline at 100 m). Slight peaks of nitrite also occurred in the vicinity of the nitracline. Phosphate concentrations exhibited more contrasted vertical profiles than did nitrate: DIP concentrations were greater than 100 nM in the surface layers of LDC, but presented a phosphacline shallower than the nitracline at LDA and LDB, with DIP reaching concentrations below the analytical detection limits in the mixed layer (i.e. < 50 nM, see Moutin et al., 2018 for more details on nutrient distribution). As DOC was not sampled on day2, DOC data are presented for the whole site instead. DOC peaked near the surface at site LDA (77 ± 1 µM) and was more variable but higher near the surface at site LDB, with maximum values covering a larger surface layer, down to 27 m, with average DOC of 84 ± 1 µM. Site LDC presented a large sub surface maximum within 28–42 m, reaching 77 ± 2 µM.

At site LDA, nitrogen was the first factor stimulating BP down to 100 m depth, which corresponded to the dcm depth and a nitrite regeneration layer. Although significant at 9, 24, 35 and 100 m depth (Mann-Whitney test, $p < 0.05$) the response to N amendments was small, at best an enrichment factor of x1.6. Glucose alone stimulated BP at 35 m but only by a factor x1.4. However, below the euphotic zone, glucose was the first factor stimulating BP (enrichment factor x2.4 at 200 m). NPG showed the largest enrichment factors, x2.5 to x3.0 and all along the profile except at 9 m were NPG amendments did not significantly affect BP compared to the control.

At site LDB, between the surface and 42 m, nitrogen alone but also phosphate alone stimulated BP to a larger extent than at site LDA, but only by a factor x1.5–3 for P, and x1.8–3.7 for N. At 100 m and 200 m, nitrogen continued to stimulate BP to a small extent (x3.0, and x2.2, respectively), but the maximum enhancement was obtained after glucose addition alone (x59, and x107, respectively). At these depths, the BP response after addition of NPG was also largely amplified compared to shallower layers (x120–132 compared to x3.7–6.8, respectively).

At site LDC, BP reacted mostly to glucose alone, with enhancement factors increasing from x2.6 at 16 m to x24 at 200 m. Nitrogen alone also stimulated BP, but to a smaller extent than glucose, even within surface layers (x1.2 to x9). In comparison to single amendments, the NPG addition particularly stimulated BP at 60 m and 90 m depth.

4 Discussion

4.1 An overview of BP and PP fluxes in the WTSP

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Here, we provide a unique, coherent dataset with simultaneous estimates of PP, BP, T_{DIP} and N_2fix rates in the WTSP. Although recent interest has increased in describing fluxes and planktonic communities responsible for N_2fix rates in diverse environments, particularly in oligotrophic open oceans, measurements in the tropical area of the South Pacific Ocean are rare (summarized in Gruber et al., 2016 and more recently Bonnet et al., 2017). Moreover, few studies have attempted to simultaneously study the consequences of such activities on the functioning of the microbial food webs.

Stations in the western part of the transect along the Melanesian Archipelago (MA) generally displayed higher fluxes of PP, BP and N_2fix rates than those in the WGY area, with a large degree of longitudinal variability. This was mirrored by by T_{DIP} variability spanning two orders of magnitude in the upper 40 m layers within MA (2 to 700 h). The role of the submesoscale activity largely explained such variabilities in biogeochemical parameters and fluxes (Rousselet et al., 2017).

Previous *in situ* measurements of primary production in the tropical south Pacific, not directly focusing on coastal areas or within upwelling areas in the East, are scarce (Table 1). These daily particulate primary production rates, based on the ^{14}C or ^{13}C technique, confirm the trend that we observed in the WTSP, i.e. extremely low values in the central GY area ranging from 8 to167 mg C m^{-2} d^{-1}. PP increased in the periphery of the GY, but rates remained typical of oligo to mesotrophic conditions, in the Eastern region of the GY, in the South of the GY, and in the western part of the WTSP around New Caledonia and between New Caledonia and Australia (Table 1). Further northwest, in the Solomon Sea, PP increased to much higher values in an area of intense nitrogen fixation, up to 3000 mg C m^{-2} d^{-1} (Table 1). However, although an increasing number of PP and N_2fix values are available in the WTSP and within the GY, the only other BP data available in these regions are those estimated during the BIOSOPE cruise (Nov./Dec. 2004), along a longitudinal transect further east between Tahiti and Chile (Van Wambeke et al., 2008b). The authors measured BP integrated across the euphotic zone ranged ranging from 86 to144 mg C m^{-2} d^{-1} within the Marquesas Archipelago, from 43 to 114 mg C m^{-2} d^{-1} within the center of the GY and from 57 to 93 mg C m^{-2} d^{-1} within the eastern part of the GY. Therefore, in the WTSP we encountered the same range of BP values than in the GY area eastern of 140°W.

4.2 BGE and Metabolic state

Although the metabolic state of oligotrophic oceans is still controversial (Duarte et al., 2013; Ducklow and Donney, 2013; Williams et al., 2013; Serret et al., 2015, Letscher et al., 2017), a consensus emerges *that in vitro* estimates (involving O_2 derived rates or labelling with $^{18}O_2$ ^{13}C, or ^{14}C isotopes) tend to show net heterotrophy in oligotrophic environments. This is indeed what we obtained here with negative NCP values at the 3 sites LDA, LDB and LDC (-97 to -198, -73 to -134 and -61 to -141 mmole O_2 m^{-2} d^{-1}, respectively, Lefevre et al., this issue). In the WTSP, negative NCP were also obtained in the oligotrophic waters off-shore of New Caledonia (Pringault et al., 2007).

However, *in vitro* technique estimates suffer from many biases related to reproductibility, bottle effects, type of flasks used (selecting light wavelengths), condition of incubations and handling artefacts, and a lack of high frequency measurements (Aranguren-Gassis et al., 2012a,b). For example following the same water mass during 5 days, a substantial variation in NCP by nearly two-fold was observed at the LDA, LDB and LDC sites. In contrast, *in situ*-based estimates, based on observations of mixed-layer net oxygen exchanges (O_2/Ar technique), tend to favour slight net autotrophy (Williams et al., 2013). However, these results also suffer from biases, related to the estimate of the mixed layer depth considered and the diffusive coefficients used for gases. Another approach based on the use of oxygen sensors in Argo floats recently showed annual NCP close to zero in the South Pacific Ocean (Yang et al., 2017). Recent models encompassing all seasons and a large areal basis find the global ocean to be net autotrophic, including all five oligotrophic subtropical gyres (Letscher et al., 2017). Estimating the metabolic balance by comparing different methods is thus of great interest but rare, especially in the South Pacific. For instance, in the center of the GY, between the Polynesian Archipelago and Easter Island,

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net heterotrophy was also obtained (although not statistically different from zero) using in vitro O_2 technique (Van Wambeke et al., 2008b), whereas a non-intrusive bio-optical method showed metabolic balance (Claustre et al., 2008a) in the same area.

Simultaneous estimates of PP, BP and N_2Fix rates are almost absent in oligotrophic waters and to date, BP has not been measured in the WTSP. Here we analyze the contribution of primary production to bacterial carbon demand by comparing separate estimates from the WTSP using our C-based discrete biological fluxes. The ratio of bacterial carbon demand (BCD) to GPP is presented as an index of the coupling between primary producers and heterotrophic bacteria and of metabolic balance (Hoppe et al 2002; Fouilland and Mostajir, 2010): to sustain heterotrophy when BCD exceeds GPP, populations can be temporally non synchronous and/or allochtonous sources of DOM may be required.

It is known that the in vitro ^{14}C method measures an intermediate state between net PP and GPP. However, Moutin et al. (1999) showed that GPP could be reasonably estimated from daily net PP determined from dusk to dusk as: GPP=1.72 * PP. On the other hand, dealing with the assumptions made to convert hourly leucine incorporation rates to daily BCD, there are many biases that have been largely debated, including mostly those resulting from daily variability, assumptions on BGE or BR (Alonzo-Saez et al., 2007; Aranguren-Gassis et al., 2012b), carbon to leucine conversion factors (Alonso-Saez et al., 2010), and light conditions of incubations including UV (Ruiz-Gonzales et al., 2013). In this study, we provide direct and indirect estimation of BGE to discuss its variability. Daily variability will be also taken into account using results from previous experiments in the South Pacific Gyre (BIOSOPE cruise, Van Wambeke et al., 2008). Finally, we will discuss one largely unexplored bias, related to the ability of *Prochlorococcus* to assimilate leucine in the dark.

Bacterial growth efficiencies (BGE) obtained from biodegradation experiments ranged 6–12 %, with a small labile fraction of DOC (only 2–5 % of biodegradable DOC in 10 days). Thus, the bulk DOC was mainly refractory, although DOC concentration was high in the surface (Moutin et al., 2018). Large stocks of DOC, with C/N ratios ranging 16 to 23 have also been reported in the surface waters of the SPG (Raimbault et al., 2008). Both high C/N ratios and a small labile fraction suggests that this surface bulk pool of DOC is probably largely recalcitrant due to UV photodegradation or photooxidation (Keil and Kirchman, 1994; Tranvik and Stephan, 1998; Carlson and Hansel, 2015) or by action of the microbial carbon pump (Jiao et al., 2010). Small BGE and small labile fraction could also be due to strong resource dependence as low nutrient concentrations cause low primary production rates, and low transfer across food webs. Indeed, Letscher et al. (2015) also observed surface DOC recalcitrant to remineralization in the oligotrophic part of the eastern tropical south Pacific. But as shown by these authors, incubation with microbial communities from the twilight zone, provided by addition of an inoculum concentrated in a small volume, allowed DOC remineralization. This was explained by relief from micronutrient limitation or by the co-metabolism of relatively labile DOC provided by the inoculums with more recalcitrant DOC. Results from our enrichment experiments effectively suggest nutrient limitation, although the second hypothesis cannot be excluded.

In order to better explain the variability of BGE measurements, we also estimated this parameter indirectly, using simultaneously measured dark community respiration (DCR) and BP. We converted DCR to carbon units assuming a respiratory quotient RQ = 0.9, and computed BGE from Ze-integrated BP and DCR assuming either bacterial respiration (BR) to be within a range of 30 % of DCR (BGE=BP/(BP+DCR*0.9*30 %)) (Rivkin and Legendre, 2001; del Giorgio and Duarte, 2002) or 80 % of DCR (BGE=BP/(BP+DCR*0.9*80 %), Le Mee et al., 2002; Aranguren-Gassis et al., 2012b). These indirect estimates of BGE ranges were similar to those obtained from the biodegradation experiments: 3–12 % at site LDA, 4–17 % at site LDB and 2–7 % at site LDC. Note, however, an increasing trend from day 1 to day 5 at site LDB: on average 8 % on day 1, 10 % on day 3 and 12 % on day 5. Including all direct and indirect estimates, the mean (± sd) BGE was 8 % ± 4 % (n=21).

Although bias introduced when converting hourly to daily BP rates was not studied here, we used a dataset obtained in the South Pacific Gyre (Van Wambeke et al., 2008) to estimate conversion errors. During the BIOSOPE cruise, vertical profiles of BP were acquired every 3 h up to 72 h, using the leucine technique within the euphotic zone at three selected sites

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using a Lagrangian sampling strategy. For the three series of profiles, standard deviations of BPI with time were 13 % (n = 13), 16 % (n = 16) and 19 % (n = 9). Thus, standard errors represented 3.6, 4.2 and 6.1 % of the mean BPI, respectively. We used the average value of this percentage (5 %) to estimate the bias introduced by the conversion from hourly to daily BPI estimates of the OUPACE cruise.

Finally, we considered the ability of *Prochlorococcus* to assimilate leucine in the dark. Using flow cytometry cell sorting of samples labelled with ^{3}H-leucine during the OUTPACE cruise, Duhamel et al. (in press) demonstrated the mixotrophic capacity of *Prochloroccoccus*, as this phytoplankton group was able to incorporate leucine even under dark conditions, albeit at lower rates than in the light conditions. This group was found to be able to assimilate ATP, leucine, methionine, and glucose a single C-containing molecule (Duhamel et al., in press, and ref therein). To date, few organic molecules have been tested and those mainly include N, P or S sources. As leucine assimilation by *Prochloroccoccus* was significantly detected in dark incubations in all examined samples, it will affect BP measurements. We thus corrected BP corrected (BP_{corr}) to represent the assimilation of leucine in the dark by heterotrophic bacteria alone. Based on Duhamel et al. (in press), leucine assimilation by HNA+LNA bacteria in the dark corresponded on average (± sd) to 76 ± 21 % (n = 5, range 44–100 %) of the activity determined for the community including *Prochlorococcus* (HNA + LNA + Proc). $I\text{-}BCD_{corr}$ was then calculated and its distribution presented with I-GPP (Figure 10), assuming a mean 8 % for BGE in all our integrated data. Among 14 stations over the 17 presented the mean integrated $I\text{-}BCD_{corr}$ is greater than I-GPP. We tested whether the confidence interval 95 % of the difference $I\text{-}BCD_{corr}$ minus I-GPP included or not zero (*t* -test) before concluding on the metabolic balance, and found that I-GPP is significantly lower than $I\text{-}BCD_{corr}$ at stations SD4, 5, 6, 12 and LDB (i.e. only 5 stations among 17), and greater at only one (SD9). Remaining stations (11 among 17) were in metabolic balance. These results confirm the necessity to include the variability of different conversion factors before making conclusions about wether GPP satisfies (or not) BCD and to account for the bias introduced by *Prochlorococcus* assimilation of leucine in BP estimates.

Such comparisons between GPP and BCD would be more complex if the short-term temporal variability in conversion factors was considered. For example, site LDB illustrates how rapidly these relative fluxes changed during the collapse of the bloom. LDB was located inside a massive chlorophyll patch, which had been drifting eastwards for several months (de Verneil et al., 2017b) and which collapsed at the time LDB was sampled. Considering the decreasing chl a stocks, decreasing PP and increasing BP, BCD_{corr} to GPP ratios would increase from 1.08 (day 1) to 1.83 (day 5), based on a constant BGE of 8 %. However, using the actual BGE increase that we observed from days 1 to 5, the ratio would increase only from 1.08 to 1.2, and the site would have been under metabolic balance during that period. Unfortunately, it is nearly impossible to assess all correction and conversion factors at the same scale that we estimated BP and PP, leading to unconstrained budgets (Gasol et al., 2008).

4.3 Nutrient limitation and relationships with nitrogen fixers

Nitrogen is primarily limiting bacterial production and primary production in the GY (Van Wambeke et al., 2008a; Halm et al., 2012). It has been shown that labile ammonium and leucine additions could stimulate N_2fix rates (Halm et al., 2012).

Phylogenetic analyses of the functional gene *nifH* showed prevalence of gamma-proteobacteria and unicellular cyanobacteria UCYN-A (presumably photo-heterotroph) in the surface layers of the ultra-oligotrophic center of the GY (Halm et al., 2012). However, quantifying gene transcripts in the GY and in the WTSP, Moisander et al. (2014) found *nifH* expression by UCYN-A to be 1–2 orders of magnitude greater than for a gamma proteobacterial diazotroph (γ-24774A11). Along the Australian great barrier reef, as determined by qPCR, the abundance of *nifH* gene copies of Gamma A group (with peaks of only 5.9×10^{2} *nifH* copies L^{-1}) were in general also 1 to 2 orders of magnitude less abundant than those of

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Trichodesmium (Messer et al 2017). Unfortunately, to date, there are no data on the *nifH* gene diversity of heterotrophic nitrogen fxers, nor on their expression, in the euphotic layers for the OUTPACE cruise, but *nifH* gene presence in some heterotrophs has been detected in the aphotic zone (Benavides et al, 2018). Using a qPCR analysis of *nifH* gene copies in selected diazotrophs, focusing on cyanobacteria (unicellular, filaments and heterocystous symbionts) during the OUTPACE cruise, Stenegren et al. (2018) showed that *Trichodesmium* dominated in surface layers (0–35m) within MA, but was rare or undetected in the WGY. Within MA the second and third most abundant populations of cyanobacteria detected were, respectively, UCYN-B and heterocystous endosymbionts (diatom-diazotroph associations). Among the investigated cyanobacterial diazotrophs, this study showed a temperature - depth gradient separating two groups of cyanobacteria, with *Trichodesmium* occupying the warmest and shallowest waters and UCYN-A occupying the coldest and deeper waters and UCYN-B having a more widespread distribution.

Regardless of the intermediary processes relating both fluxes, the amount of N_2 fixed corresponded to 15–83 % of heterotrophic bacterial nitrogen demand in MA and 3–34 % in the WGY (Figure 3b). This fraction could be particularly high in the MA area, where N_2fix rates reached maximum values for the cruise (1 mmole m^{-2} d^{-1} at station SD11). Besides this exception, the activity of N_2 fixers generally sustained less than half the heterotrophic bacterial N demand (mean ± sd: 34 ± 20 %, n = 26). Nevertheless, the activity of N_2 fixers is responsible for the injection of new N in the microbial food chain, enabling a cascade transfer through non-fixing autotrophs and heterotrophs, and possibly C and N export by sedimentation even in oligotrophic areas of the WTSP (Caffin et al., 2017). The transfer between N_2 fixers and heterotrophic prokaryotes occurs on a daily scale, as confirmed by nano-scale secondary ion mass spectrometry (nanoSIMS) experiments, which make it possible to track the fate of $^{15}N_2$ at the individual cell level. These experiments have shown a rapid N transfer from *Trichodesmium* colonies to heterotrophic epiphyte bacterial cells (Eichner et al., 2017). Although it is not known from this study if the ^{15}N can reach free living heterotrophic prokaryotes or non-fixing phytoplankton, other experiments suggest that ^{15}N fixed by *Trichodesmium* reaches rapidly non-fixing diatoms (Foster et al., 2011; Bonnet et al., 2016). Using artificial diazotroph cultures inoculated in natural sea waters from the New Caledonia lagoon, Berthelot et al. (2016) showed also a rapid transfer (48h) from a *Trichodesmium* (*T. erythraeum*) and a UCYN-B (*Chrocosphaera. Watsonii*) towards heterotrophic bacteria. Recent evidence also suggests a rapid transfer from the symbiotic photo-heterotrophic cyanobacterium UCYN-A, which have much greater growth rates than *Trichodesmium*, to its associated eukaryotic algae (Martinez-Perez et al., 2016).

Consequently, most N_2 fixing cyanobacteria detected in the WTSP during this cruise have a potential to transfer N rapidly (1–2 days) towards strict heterotrophic bacteria or non-fixing phytoplankton. We found that the correlation between N_2fix rate and BP was better within the mixed layers and when the T_{DIP} is low (< 100 h), i.e. in areas of phosphate deficiency (Moutin et al., 2008). Greater correlation between BP and N_2fix than between BP and PP would suggest that bacteria may have been more dependent on the availability of new source of N than C, which is in agreement with results from enrichment expriments at LDA and LDB. Because T_{DIP} was lower in areas of high N_2fix rates, it is likely that DIP drawdown was due to diazotrophs which while bringing new sources of N, reduced DIP availability. Indeed, at site LDB within the mixed layers, BP is increased after N addition alone but also after P addition alone, which suggest a direct N limitation of BP by N and potentially a cascade effect after P addition towards heterotrophic prokaryotes; P would directly stimulate N_2 fixers which rapidly would transfer new N and labile C available to stimulate BP. At sites LDA and LDB, the addition of the 3 elements NPG stimulated BP more than P alone or N alone, suggesting possible NP co-limitation of heterotrophic prokaryotes. Furthermore, if N was shown to be the first limiting nutrient during short time scale experiment, addition of P stimulates N_2fix, PP and export at larger time scales (Van Den Brock et al., 2004; Berthelot et al., 2015, Gimenez et al., 2016).

Below the surface layers, where T_{DIP} increases, and where UCYN-A dominates, DIP becomes available, and nitrate diffusing through the nitracline sustains primary production, BP and PP were correlated within these layers, suggesting a

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strong coupling between BP and PP through the release of labile organic C. Indeed, our enrichment experiments revealed that BP was limited fist by labile C, secondarily by N within these layers (Fig. 9).

Finally, within the WGY area, where T_{DIP} were elevated in the mixed layer (more than 100 h), with detectable DIP concentrations reaching 100 nM, the activity of N_2 fixers was extremely low. In this area, BP was limited mainly by the availability of energy or labile C. Indeed, within site LDC, glucose alone stimulated BP on a larger extent than did N alone, even when the latter was provided in the form of ammonium. This trend was also observed from enrichment experiments made in the center and the eastern zones of the GY (Van Wambeke et al., 2008a). UCYN-B dominated the N_2 fixing populations in the WGY, which accounted for 81–100 % of the total detected cyanobacterial *nifH* gene copies (Stenegren et al., 2018). Among UCYN-B, *Crocosphaer*a is one of the most studied representatives. One of its sub-populations is recognized to produce EPS (Bench et al., 2016), which could be a significant energy source for heterotrophic prokaryotes. In the North Pacific Subtropical gyre, Wilson et al (2017) hypothesized that *Crocosphaer*a could fix N_2 in excess of its growth requirements and could leak fixed N in seawater. They also showed a highly dynamic of *Crocosphaer*a growth and decay during diel cycles, suggesting rapid switch between cell growth and mortality processes, such as grazing and viral infection. The resources provided by leakage, lysis and grazing process likely directed energy and N towards heterotrophic bacteria at a daily scale when N_2 fixation is favourable, as in the North Pacific. However, in the WGY, rates of N_2fix rates are very low and could only sustain a low percentage of bacterial and phytoplankton N demand.

5 Conclusion

Our results provide a unique set of simultaneous measurements of BP, PP and N_2fix rates in the WTSP. BP obtained in the WTSP was in the same range as those previously measured in the GY area east of 140°W. BGE was low (8 % on average) and the bulk DOC was found to be refractory (labile DOC 2-5 % on average). We show that the interpretation of PP and BP fluxes based on instantaneous methods (radioisotopic labelling) needs regular tests to verify the major methodological biases. In particular, to make conclusions about the metabolic state of oceanic regions, it is necessary to consider the variability of all conversion factors used to estimate carbon-based GPP and BCD. In addition, the use of the leucine technique to estimate BP should be used with caution in N-limited environments due to the potential mixotrophy by cyanobacteria. Taking these corrections into account and using propagation of errors, we compared I-BCD_{corr} and I-GPP as indexes of the coupling between primary producers and heterotrophic bacteria. We found that the system was in metabolic balance at 11 over the 17 stations investigated. In the N and relatively DIP depleted surface waters, BP was more strongly correlated to N_2fix than to PP, while the more traditional coupling of BP with PP occurred deeper in the euphotic zone. This suggests that in surface layers with elevated diazotrophic activity, BP was more dependent on the availability of new N from the activity of N_2 fixers than on the availability of fresh C from the activity of primary producers, as was also demonstrated through enrichment experiments.

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Déplacé vers le haut [8]: We show that the interpretation of fluxes based on instantaneous methods (radioisotopic labelling) needs regular tests to verify the major methodological hypothesis, in particular, the use of the leucine technique to estimate BP should be used with caution in N-limited environments due to the potential mixotrophy by cyanobacteria. The variability of bacterial carbon demand and gross primary production rates measured in this study reveal the highly diverse metabolic status of the WTSP.
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Table 1. Review of Integrated primary production rates published in the South Pacific, PP fluxes in mg C m^{-2} d^{-1}. Only open sea data were included.

Area	Latitude	Longitude	Number of stations	Period	Technique	PP fluxes mg C m^{-2} d^{-1}	Reference
Solomon Sea	3–9°S	146–152°E	12	Feb/March 14	13C, GF/F, deck	204–1116	Ganachaud et al., 2017
Solomon Sea	5–12°S	147–165°E	15	June/Aug 12	13C, GF/F, deck	480–1200	
Eastern Australia off shore	27–29°S	160–162°E	2	Sept 04	14C, GF/F, deck.	260–910	Young et al., 2011
New Caledonian	17–23°S	157–170°E	7	July-Aug 11	14C, 0,4 µm PC, P vs I	352 ± 160	Menkes et al., 2015
Exclusive Econ. Zone	17–23°S	157–170°E	5	nov-dec 11	14C, 0,4 µm PC, P vs I	231 ± 133	
Melanesian Archipelago	18–19°S	159°E–170°W	14	Feb/March 15	14C, 0.2 µm PC, deck	148–858	Moutin et al., 2017, this study
Marquesas archipelago	8–13°S	140–130°W	5	Nov-Dec 04	14C, 0.2 µm PC, deck	250–680	Van Wambeke et al., 2008a
Western GY	18°S	169–149°W	4	Feb/March 15	14C, 0.2 µm PC, deck	55–208	Moutin et al., 2017, this study
Center GY	15–30°S	130–100°W	11	Nov-Dec 04	14C, 0.2 µm PC, deck	76–167	Van Wambeke et al, 2008a
Center GY	25–26°S	104–100°W	2	Nov-Dec 10	14C, 0.2 µm PC, deck	216–276	Rii et al, 2016
Center GY	23–27°S	165–117°W	7	Dec 06-Jan 07	13C, GF/F, deck	8–33	Halm et al., 2012
Southern rim of the GY	38–41°S	153–133°W	3	Dec 06-Jan 07	13C, GF/F, deck	79–132	Halm et al., 2012
East GY	30–33°S	95–78°W	6	Nov-Dec 04	14C, 0.2 µm PC, deck	195–359	Van Wambeke et al., 2008a
East GY	23°S	88°W	1	Nov-Dec 10	14C, 0.2 µm PC, deck	600	Rii et al., 2016

Table 2. Physical and biological characteristics of main biogeochemical areas and long duration stations sampled during the OUTPACE cruise. Depth of the dcm (deep chlorophyll maximum, based on vertical profiles of in vivo fluorescence), σt: sigma-theta at the dcm (kg m^{-3}), Ichl a (integrated chlorophyll a from fluorometric discrete analyses on extracted samples), IN_2 fix (integrated N_2 fixation rates), IPP (integrated primary production), IBP (integrated bacterial production at the depth of the euphotic zone), DCR (dark community respiration integrated over the euphotic layer). WMA clustered stations SD1, 2, 3 and LDA, EMA clustered SD 6, 7, 9 and 10, WGY clustered SD13, 14, 15 and LDC. In order to encompass only spatial variability for WMA, EMA and WGY groups of stations, means and ranges of dcm depths and of σt at the dcm depth were based on the averages values set individually at each SD or LD stations as more than one cast was sampled per station. Means ± sd and range values given for LDA, LDB and LDC illustrate the temporal variability at LD sites: all ctd casts sampled at each LD site down to 200 m were included.
[*] values from Bonnet et al. (2018) and Caffin et al. (2017) also presented in Fig. 3b.
[**] values from Moutin et al. (2018) also presented in Fig. 2 and Fig. 3a.
[***] at station SD13, BP and N_2fix rates were not measured; PP obtained was abnormally low (55 mg C m^{-2} d^{-1}) and excluded from the mean.

		WMA	EMA	WGY	LDA	LDB	LDC
dcm depth	mean ± sd (n)	82 ± 10 (4)	105 ± 10 (4)	136 ± 14 (4)	81 ± 9 (46)	50 ± 18 (47)	131 ± 7 (46)
m	range	72 – 91	9 1– 115	123 – 154	63 – 101	10 – 77	115 – 154
σt at the dcm	mean ± sd (n)	23.8 ± 0.4 (4)	24.2 ± 0.3 (4)	24.53 ± 0.09 (4)	23.55 ± 0.05 (46)	23.1 ± 0.7 (47)	24.62 ± 0.02 (46)
kg m^{-3}	range	23.5–24.3	23.8–24.6	24.4 – 24.6	23.47 – 23.64	21.7 – 23.9	24.59 – 24.67
Ichl a	mean ± sd (n)	na	28.7 ± 6.2 (4)	18.1 ± 4.5 (4)	26.0 ± 2.6 (5)	38.9 ± 10.4 (5)	16.2 ± 1.3 (7)
mg Chl a m^{-2}	range		23.6–37.8	13.2 – 23.6	23.7 – 29.6	23.9 – 53.2	14.0 – 17.7
IN_2fix (deck)	mean ± sd (n)	0.65 ± 0.21 (4)[*]	0.50 ± 0.27 (4)[*]	0.09 ± 0.08 (3)[***]			
nmole N m^{-2} d^{-1}	range	0.48–0.96	0.21–0.85	0.02–0.17	0.63[*]	0.94[*]	0.07[*]
IN_2fix (in situ)	mean ± sd (n)				0.59 ± 0.05 (3)[*]	0.70 ± 0.30 (3)[*]	0.06 0.01 (3)[*]
nmole N m^{-2} d^{-1}	range				0.53–0.63	0.38–0.98	0.05–0.08
IPP_{deck}	mean ± sd (n)	481 ± 147 (4)[**]	471 ± 276 (4)[**]	154 ± 55 (3) [***]			
mg C m^{-2} d^{-1}	range	367–698	192–853	104 – 213	698[*]	383[*]	213[*]
$IPP_{in\ situ}$	mean ± sd (n)				267 ± 79 (3)[*]	436 ± 72 (3) [*]	155 ± 8 (3)[*]
mg C m^{-2} d^{-1}	range				200 – 354	361 – 507	149 – 165
IBP within Ze	mean ± sd (n)	99 ± 15 (4)	95 ± 12 (4)	33 ± 2 (3) [***]	98 ± 16 (5)	113 ± 15 (6)	45 ± 5 (6)
mg C m^{-2} d^{-1}	range	82–120	80 – 110	31 – 35	81 – 115	86 – 133	38– 50
DCR	mean ± sd (n)	nd	nd	nd	226 ± 44 (3)	172 ± 18 (3)	147 ± 38 (3)
mmol O_2 m^{-2} d^{-1}	range				182-269	151-185	103-176

Table 3. Results of multiple regressions log BP=f (log PP, log N_2fix). BP Units before log- transformation is ngC l^{-1} h^{-1}. Y int is the intercept with the Y axis. Partial coefficient of regression (part coeff), t value (t) and probability of the regression to be significant (p).

Units before log transformation		mgC m^{-3} d^{-1}	nmole N l^{-1} d^{-1}			
independent variables		PP	N_2fix	Y int	n	r
$T_{DIP} \leq 100h$	part coeff ± sd	0.23 ± 0.11	0.38 ± 0.10	-0.56	36	0.589
	t (p)	2.04 (0.02)	3.82 (0.0002)			
$T_{DIP} > 100h$	part coeff ± sd	0.43 ± 0.08	0.09 ± 0.05	-0.47	51	0.66
	t (p)	4.91 (< 0.0001)	1.82 (ns)			

Table 4. Results of multiple regressions log T_{DIP}=f (log BP, log PP, log N_2fix). Units of T_{DIP} before log-transformation is h. Y int is the intercept with the Y axis. Partial coefficient of regression (part coeff), t value (t) and probability of the regression to be significant (p)

Units before log transformation		ngC l^{-1} h^{-1}	nmol N l^{-1} d^{-1}	mgC m^{-3} d^{-1}			
independent variables		BP	N_2fix	PP	Y int	n	r
All data	part coeff ± sd	-1.06 ± 0.2	-0.23± 0.07	-0.18 ± 0.15	3.82	91	0.81
	t	-5.2	-3.1	-1.2			
	(p)	(p< 0.0001)	(p=0.0027)	(ns)			
Depth ≤ 20m	part coeff ± sd	-1.11 ±0.34	-0.07 0.13	0.54± 0.27	3.88	47	0.76
	t	-3.2	-0.5	1.97			
	(p)	(p= 0.0024)	(ns)	(ns)			

Table 5. Results of biodegradation experiments. Growth rates determined from BP data, degradation rates computed from DOC data and BGE computed from eq 1.

	LDA	LDB	LDC
growth rates ± s.e. (h^{-1})	0.33 ± 0.05	0.08 ± 0.02	0.14 ± 0.02
degradation rates ± s.e. (d^{-1})	0.039 ± 0.002	0.07 ± 0.007	0.012 ± 0.003
initial DOC stock (µM)	83	83	75
% labile DOC	5.3	5	2.4
BGE (%)	12.9	6.3	6.7

Figure legends

Figure 1 Position of stations during the OUTPACE cruise. The white line shows the vessel route (data from the hull-mounted ADCP positioning system). In dark green WMA (Western Melanesian Archipelago) including SD1, 2, 3 and LDA; in light green, EMA: eastern Melanesian Archipelago including SD6, 7, 9 and 10 and in blue WGY (Western sub tropical gyre) including stations SD13, 14, 15 and LDC. Figure courtesy of T. Wagener.

Figure 2 Distribution of primary production (a) and heterotrophic prokaryotic production (b) along the OUTPACE cruise transect, WMA (dark green), EMA (light green) and WGY (blue) stations are noted by colored reactangles. Interpolation between sampling points in contour plots was made with the Ocean Data View software (VG gridding algorithm, Schlitzer, 2004). In order to be homogeneous for the whole transect, for sites LDA, LDB and LDC, the data plotted for PP was from a single profile, that of PP_{deck}, while for BP we plotted all profiles. The white dots in (a) correspond to the average ± sd of the dcm depth at each station. The white rectangles mask abnormal extrapolation due to the absence of PP data.

Figure 3 a) Distribution of integrated heterotrophic prokaryotic production (IBP) and primary production (IPP_{deck}) along the transect, data were integrated down to the euphotic zone. WMA (dark green), EMA (light green) and WGY (blue) stations are noted by colored rectangles. b) Distribution of integrated N_2 fixation rates and of ratio N_2 fixation rates to bacterial nitrogen demand (I-N2fix/I-BND, assuming a bacterial C/N ratio of 5 and no nitrogen excretion) and along the transect. Data were integrated down to the deepest sampled depth for N_2 fixation rates. Data plotted for sites LDA, LDB and LDC correspond to BP, PP_{deck} and N_2fix measured on day 5. Error bars are standard errors (s.e.) derived from triplicate measurements at each depth (BP, PP_{deck}, N_2fix rates). For BP, error bars also take into account the daily variability, and final s.e. were calculated after propagation of errors. PP obtained at SD13 was abnormally low (55 mg C m^{-2} d^{-1}) and was excluded; BP and N_2fix rates were not measured at this station.

Figure 4 Vertical distributions of phosphate turnovertimes (T_{DIP}), in groups of stations WGY (a), WMA (b), EMA (c) and other stations (d). At the long-duration sites LDA, LDB and LDC, T_{DIP} profiles were determined at day 5 (bold lines). Horizontal bar in b (WMA) and c (EMA) delineates the mean phosphacline depth (mean ± sd: 20 ± 7 m, and 44 ± 10 m, respectively) as determined by Moutin et al. (2018). At WGY (a), DIP concentrations were > 100 nM at all depths.

Figure 5 Evolution of surface PAR (a), in vivo fluorescence and pycnoclines (b), PP (c) and BP (d) at the site LDA. Time units in local time, day1 was February 26, 2015. BP samples were taken at the 12:00 AM ctd cast, while samples for $PP_{in\ situ}$ were taken at the 3:00 AM ctd casts (day 1, 3 and 5). On graph (b), in vivo fluorescence is in color, pycnoclines (kg m^{-3}) are the white lines and vertical bars show the 12:00 AM ctd cast sampled for BP each day (1 to 5) with corresponding colours used for plotting BP vertical profiles in (d).

Figure 6 Evolution of surface PAR (a), in vivo fluorescence and pycnoclines (b), PP (c) and BP (d) at the site LDB. Time units in local time, day1 was March 15, 2015. BP samples were taken at the 12:00 AM ctd cast, while samples for $PP_{in\ situ}$ were taken at the 3:00 AM ctd casts (day 1, 3 and 5). On graph (b), in vivo fluorescence is in color, pycnoclines (kg m^{-3}) are the white lines and vertical bars show the 12:00 AM ctd cast sampled for BP each day (1 to 5) with corresponding colours used for plotting BP vertical profiles in (d).

Figure 7 Evolution of surface PAR (a), in vivo fluorescence and pycnoclines (b), PP (c) and BP (d) at the site LDC. Time units in local time, day1 was March 23, 2015. BP samples were taken at the 12:00 AM ctd cast, while samples for $PP_{in\ situ}$ were taken at the 3:00 AM ctd casts (day 1, 3 and 5). On graph (b), in vivo fluorescence is in color, pycnoclines (kg m^{-3}) are the white lines and vertical bars show the 12:00 AM ctd cast sampled for BP each day (1 to 5) with corresponding colours used for plotting BP vertical profiles in (d).

Figure 8 Log-log relationships between volumetric rates of heterotrophic prokarytotic production (BP) and primary production (PP, a) and between BP and nitrogen fixation rates (N_2fix, b). Red and black dots show samples where T_{DIP} were above and below 100 h, respectively. Lines are fitted Tessier model II regressions for data clustering samples where Tdip values were higher (black lines) and lower (red lines) than 100 h.

Figure 9 Enrichment experiments. Initial conditions illustrated by vertical profiles (0-200 m) of in vivo fluorescence, BP, nutrients (nitrate (NO3), nitrite (NO2), and phosphate (DIP)) and enrichment factors sampled from the 12:00 AM ctd cast on day 2 of occupation at each LD site. As DOC was not sampled on this cast, we showed the data from all the other casts at the corresponding LD site (circles) and the average profile (line). Enrichment factors are the ratio of BP after a given enrichment (DIP: P in red; nirate+ammonium :N in green, glucose: G in blue, and all componenrs: NPG in black) compared to the unamended control, both measured 24 h after incubations. The error bar is standard deviation within triplicates, and a bar is shown only if BP is significantly higher than in the control (Mann-Whitney test, $p < 0.05$).

Supprimé: Histogram d
Supprimé: Histogram d
Supprimé: bacterial nitrogen demand
Supprimé:
Supprimé: (
Supprimé: N_2 fixation rates
Supprimé: ,
Supprimé: d
Supprimé: .
Supprimé: Dotted profiles correspond to SD13, 14 15 and site C.
Supprimé: chl in vivo
Supprimé: chl in vivo
Supprimé:
Supprimé: chl in vivo
Supprimé:
Supprimé: panel
Supprimé: pane
Supprimé: , ammonium (NH4)
Supprimé: (PO4
Supprimé: CTD
Supprimé: dots
Supprimé: sd

Figure 10 Distribution of integrated bacterial carbon demand corrected for *Prochlorococcus* assimilation (I-$BCD_{corr,}$ grey bars) and gross primary production (I-GPP, blue bars) along the transect. Error bars are standard errors (s.e.), calculated using propagation of errors. We included analytical s.e. (triplicate measurement at each depth for PP and BP), s.e. due to daily BP variability, s.e. from BGE, and s.e. due to leucine assimilation by *Prochlorococcus*. * shows stations in which I-BCDcorr minus I-GPP was statistically different from zero.

Supprimé: Histogram d

Supprimé: heterotrophic prokaryotic production

Supprimé: IBP_{corr}

Supprimé: , left scale

Supprimé: , right scale

Supprimé: Scales of BP_{corr} and GPP are proportional by a factor 100/8 so that GPP scale is also that of BCD, and thus blue bar higher than grey bar means GGP higher than bacterial carbon demand.¶

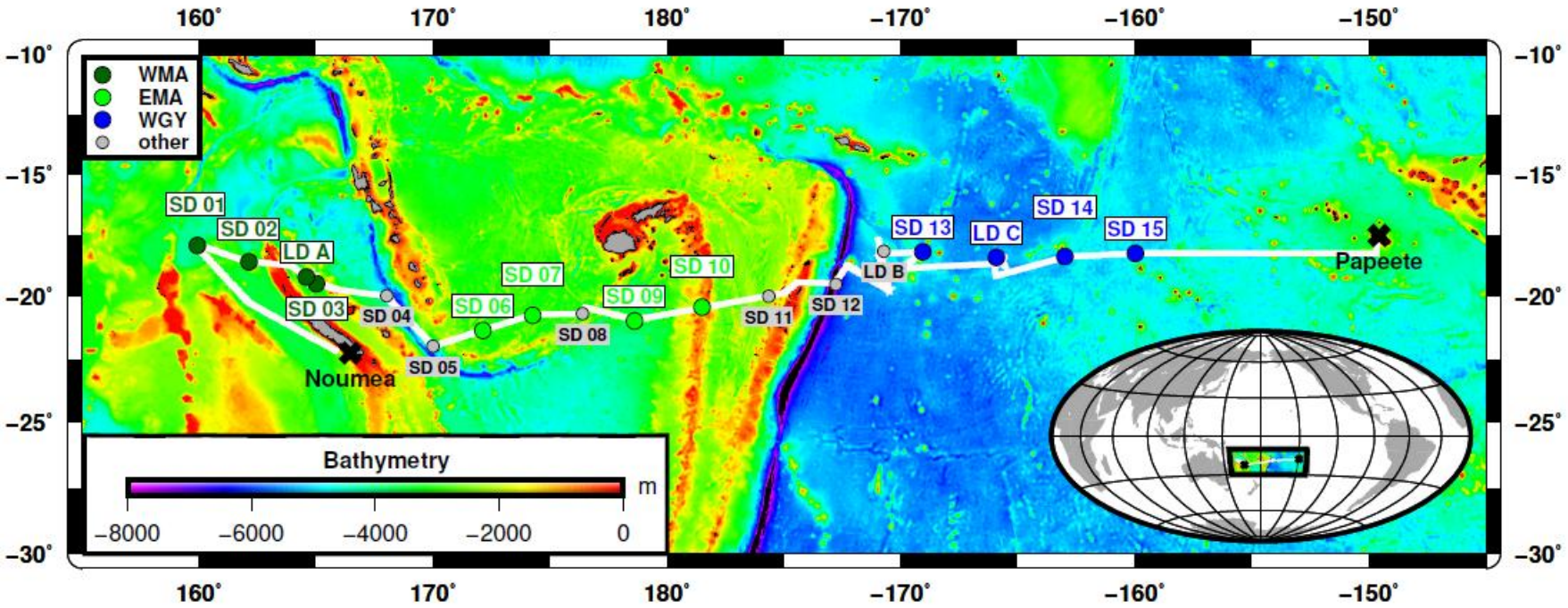

160°
170°
180°
−170°
−160°
−150°
−10°
−15°
−20°
−25°
−30°
WMA
EMA
WGY
other
SD 01
SD 02
LD A
SD 03
SD 04
SD 05
SD 06
SD 07
SD 08
SD 09
SD 10
SD 11
SD 12
LD B
SD 13
LD C
SD 14
SD 15
Noumea
Papeete
Bathymetry
m
−8000
−6000
−4000
−2000
0

Fig 1

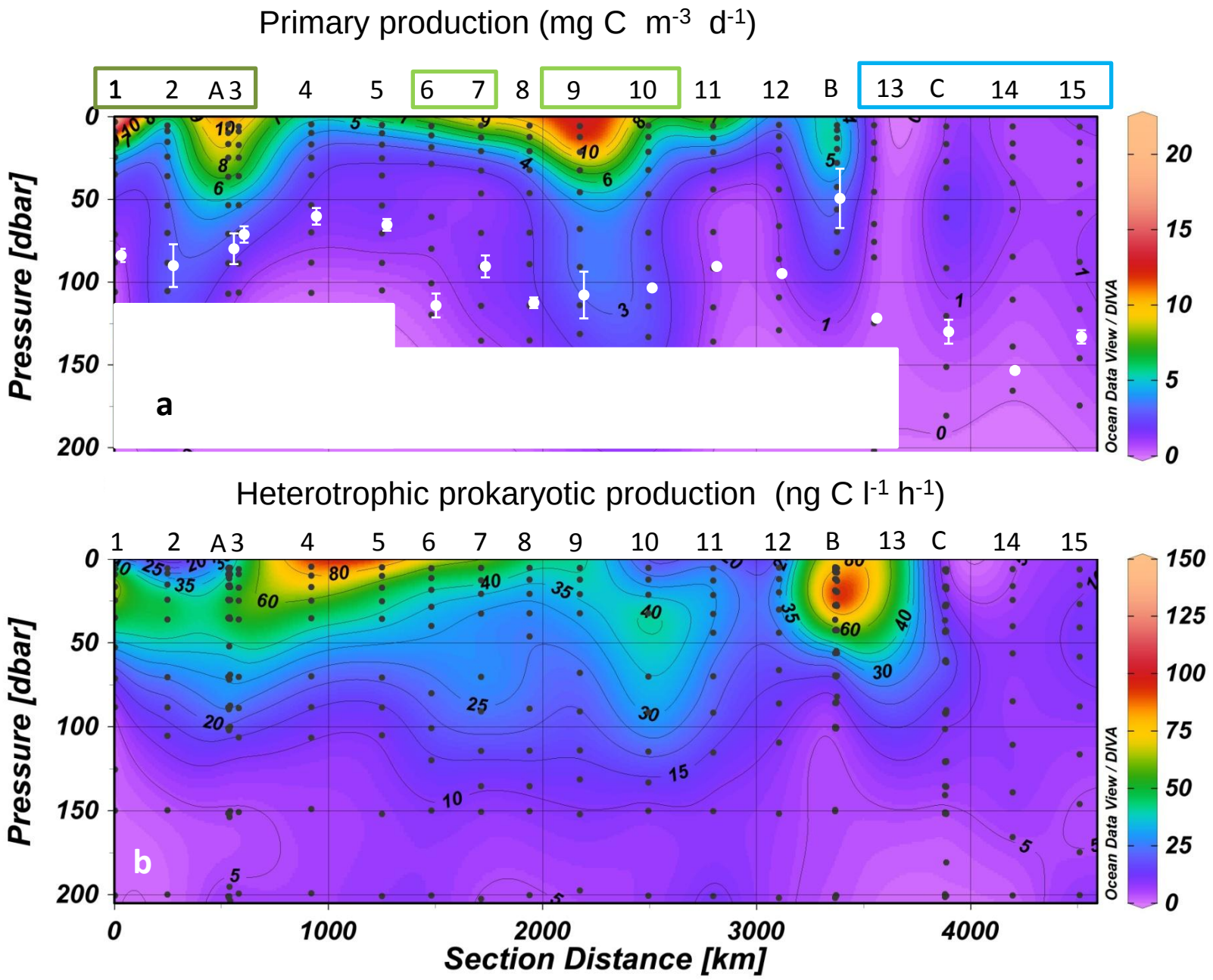

Primary production (mg C m-3 d-1)
1 2 A 3 4 5 6 7 8 9 10 11 12 B 13 C 14 15
Pressure [dbar]
0
50
100
150
200
a
Ocean Data View / DIVA
20
15
10
5
0
Heterotrophic prokaryotic production (ng C l-1 h-1)
1 2 A 3 4 5 6 7 8 9 10 11 12 B 13 C 14 15
Pressure [dbar]
b
Ocean Data View / DIVA
150
125
100
75
50
25
0
0
1000
2000
3000
4000
Section Distance [km]

Fig 2

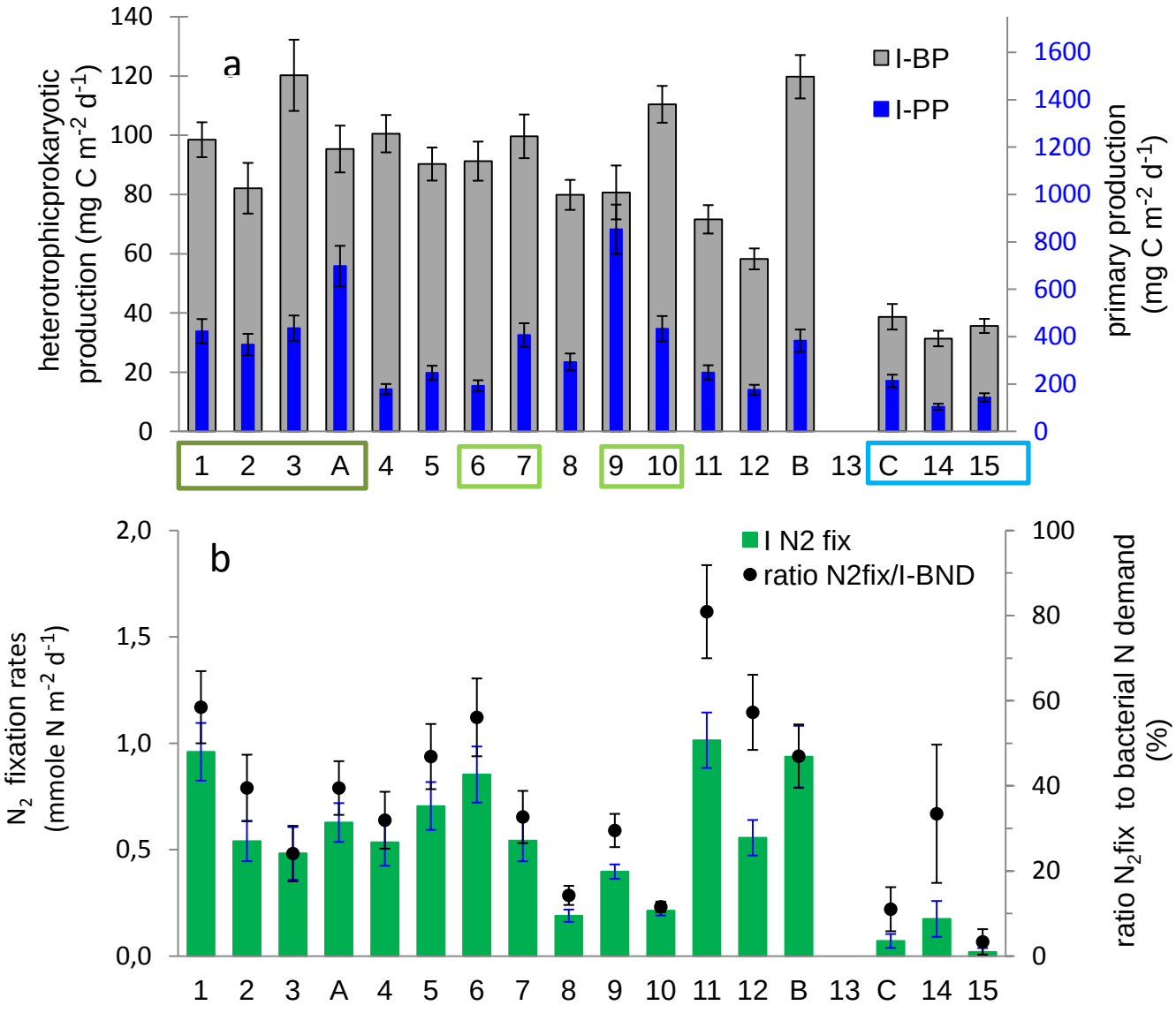

a
heterotrophicprokaryotic production (mg C m-2 d-1)
primary production (mg C m-2 d-1)
I-BP
I-PP
140
120
100
80
60
40
20
0
1600
1400
1200
1000
800
600
400
200
0
1 2 3 A 4 5 6 7 8 9 10 11 12 B 13 C 14 15
b
N2 fixation rates (mmole N m-2 d-1)
ratio N2fix to bacterial N demand (%)
I N2 fix
ratio N2fix/I-BND
2,0
1,5
1,0
0,5
0,0
100
80
60
40
20
0
1 2 3 A 4 5 6 7 8 9 10 11 12 B 13 C 14 15

Fig 3

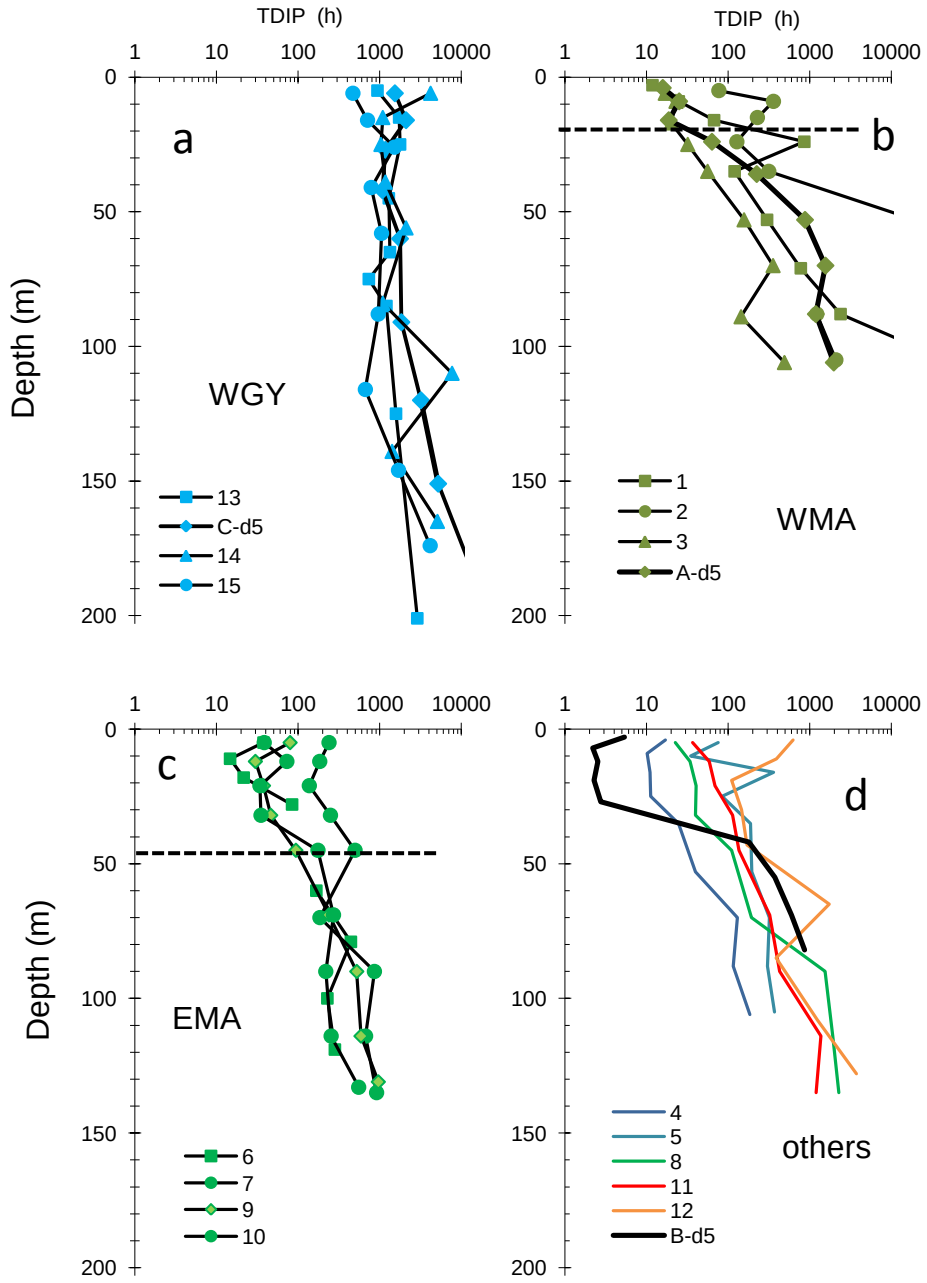

TDIP (h)
1
10
100
1000
10000
0
50
100
150
200
Depth (m)
a
WGY
13
C-d5
14
15
b
WMA
1
2
3
A-d5
c
EMA
6
7
9
10
d
others
4
5
8
11
12
B-d5

Fig 4

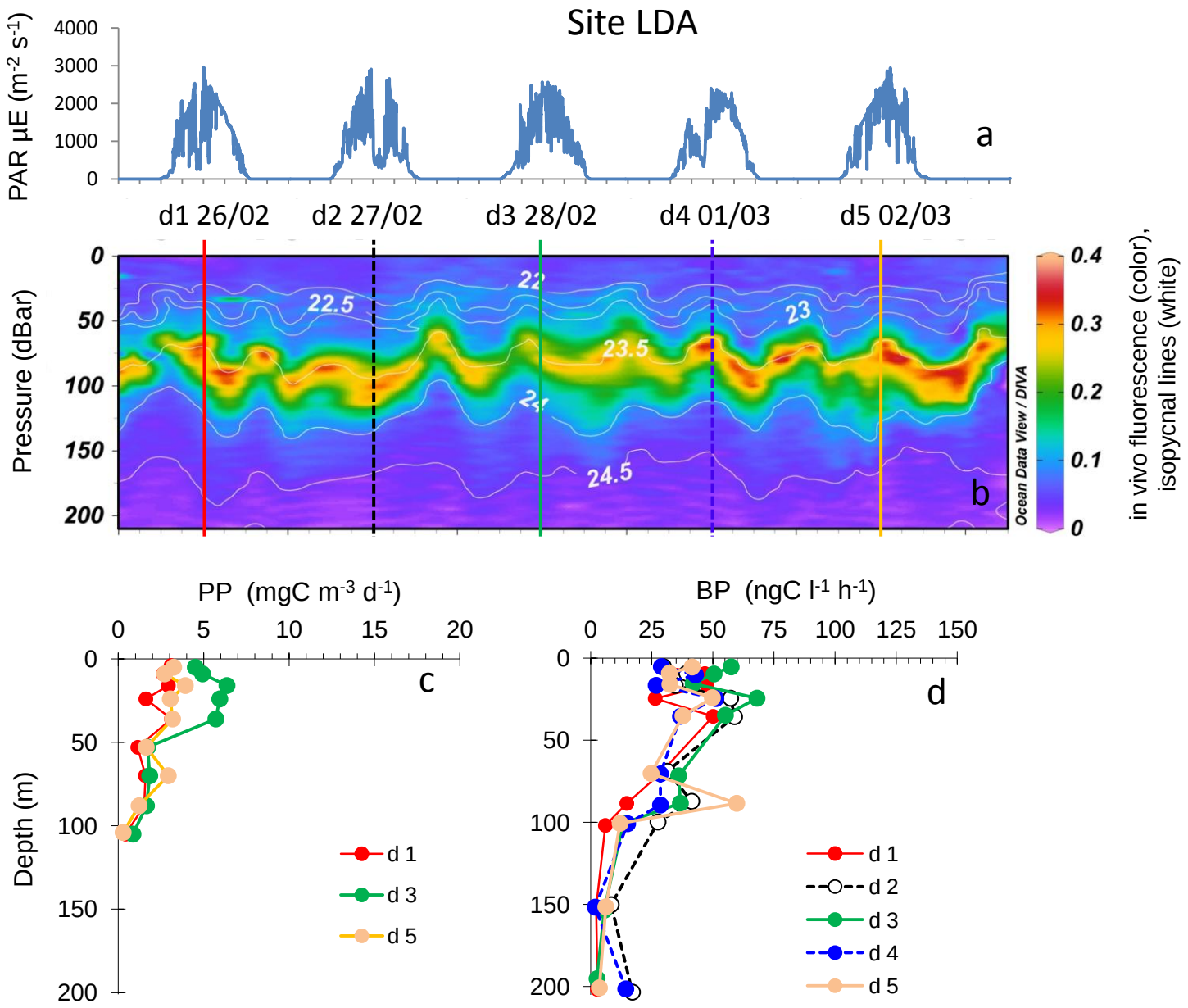

Site LDA
PAR µE (m-2 s-1)
4000
3000
2000
1000
0
a
d1 26/02
d2 27/02
d3 28/02
d4 01/03
d5 02/03
Pressure (dBar)
0
50
100
150
200
22.5
22
23
23.5
24
24.5
b
Ocean Data View / DIVA
0.4
0.3
0.2
0.1
0
in vivo fluorescence (color), isopycnal lines (white)
PP (mgC m-3 d-1)
0
5
10
15
20
c
Depth (m)
d 1
d 3
d 5
BP (ngC l-1 h-1)
0
25
50
75
100
125
150
d
d 1
d 2
d 3
d 4
d 5

Fig 5

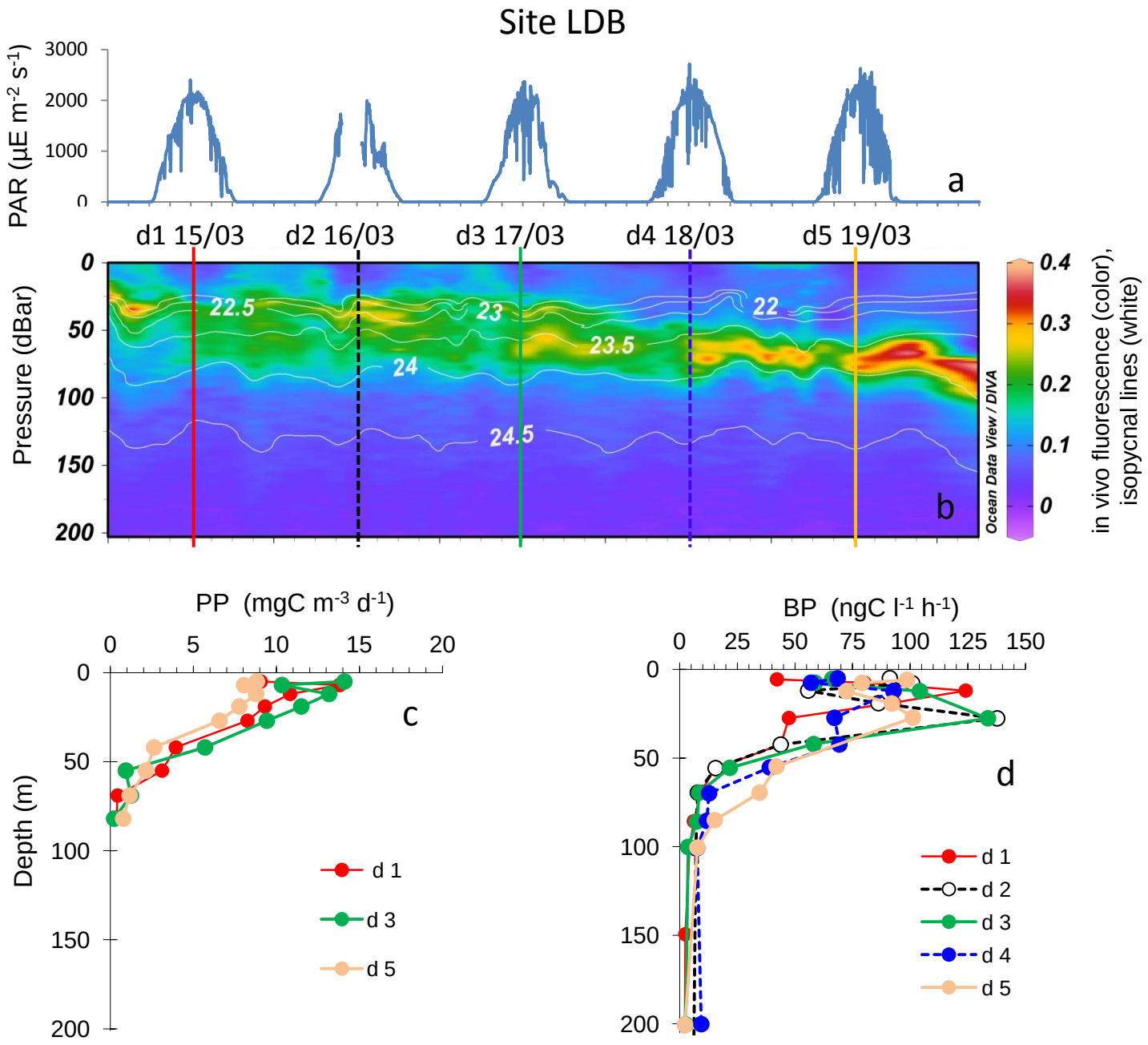

Site LDB
PAR (µE m-2 s-1)
3000
2000
1000
0
a
d1 15/03
d2 16/03
d3 17/03
d4 18/03
d5 19/03
Pressure (dBar)
0
50
100
150
200
22.5
23
24
23.5
22
24.5
b
Ocean Data View / DIVA
0.4
0.3
0.2
0.1
0
in vivo fluorescence (color), isopycnal lines (white)
PP (mgC m-3 d-1)
0
5
10
15
20
Depth (m)
c
d 1
d 3
d 5
BP (ngC l-1 h-1)
0
25
50
75
100
125
150
d
d 1
d 2
d 3
d 4
d 5

Fig 6

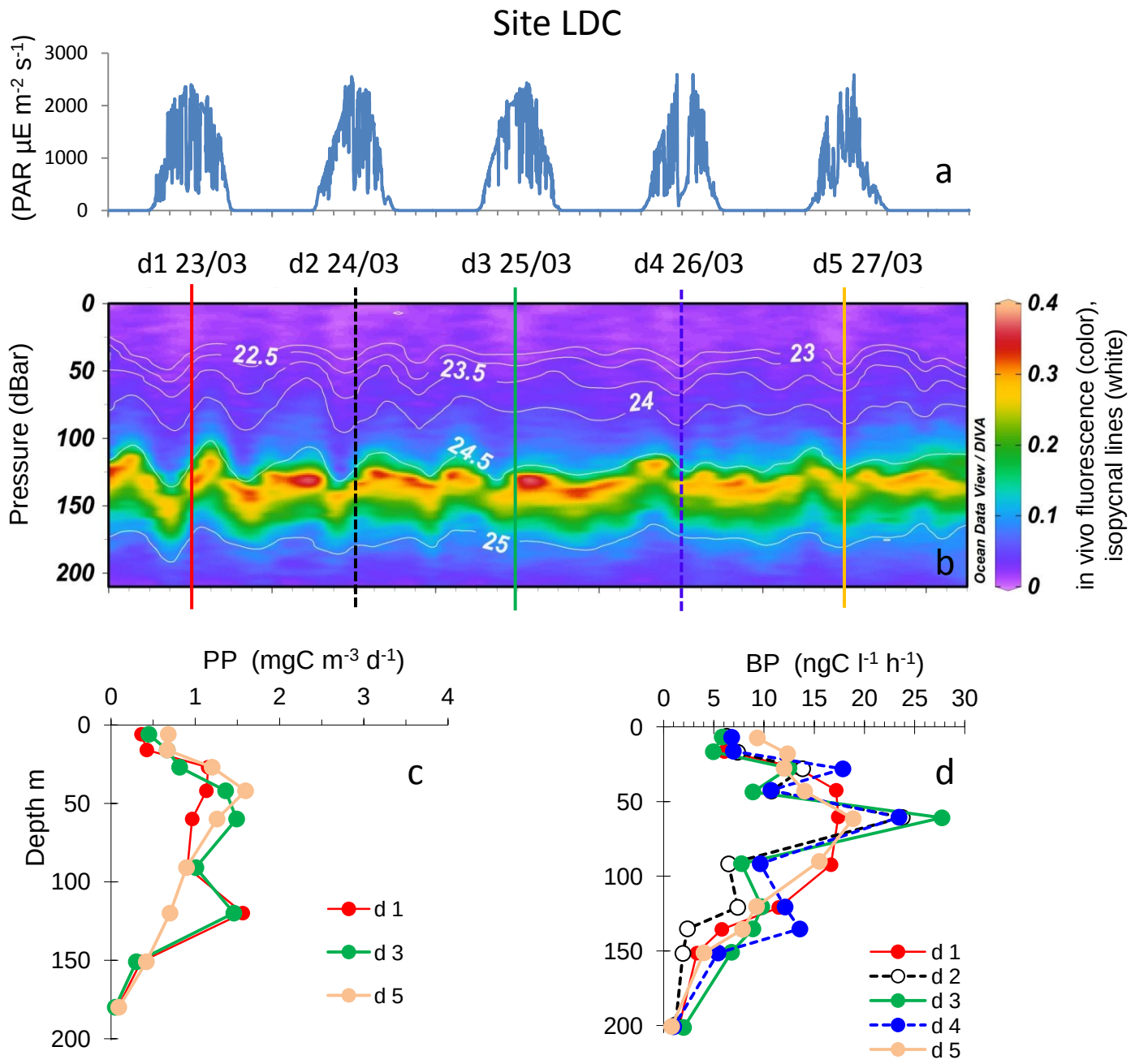

Site LDC
(PAR µE m-2 s-1)
3000
2000
1000
0
a
d1 23/03
d2 24/03
d3 25/03
d4 26/03
d5 27/03
Pressure (dBar)
0
50
100
150
200
22.5
23.5
24
24.5
25
23
b
Ocean Data View / DIVA
0.4
0.3
0.2
0.1
0
in vivo fluorescence (color), isopycnal lines (white)
PP (mgC m-3 d-1)
0
1
2
3
4
Depth m
c
d 1
d 3
d 5
BP (ngC l-1 h-1)
0
5
10
15
20
25
30
d
d 1
d 2
d 3
d 4
d 5

Fig 7

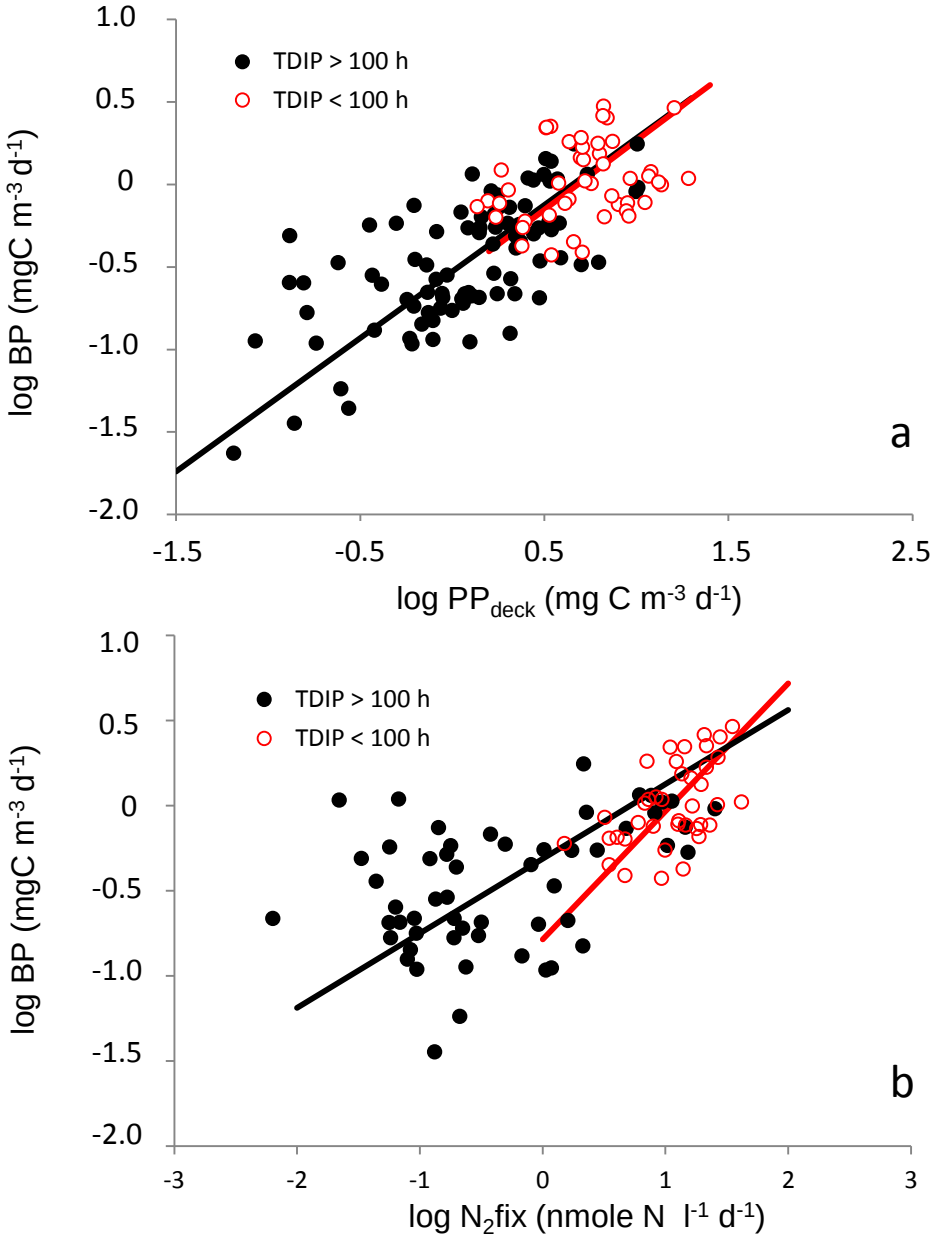

TDIP > 100 h
TDIP < 100 h
log BP (mgC m-3 d-1)
log PPdeck (mg C m-3 d-1)
a
TDIP > 100 h
TDIP < 100 h
log BP (mgC m-3 d-1)
log N2fix (nmole N l-1 d-1)
b

Fig 8

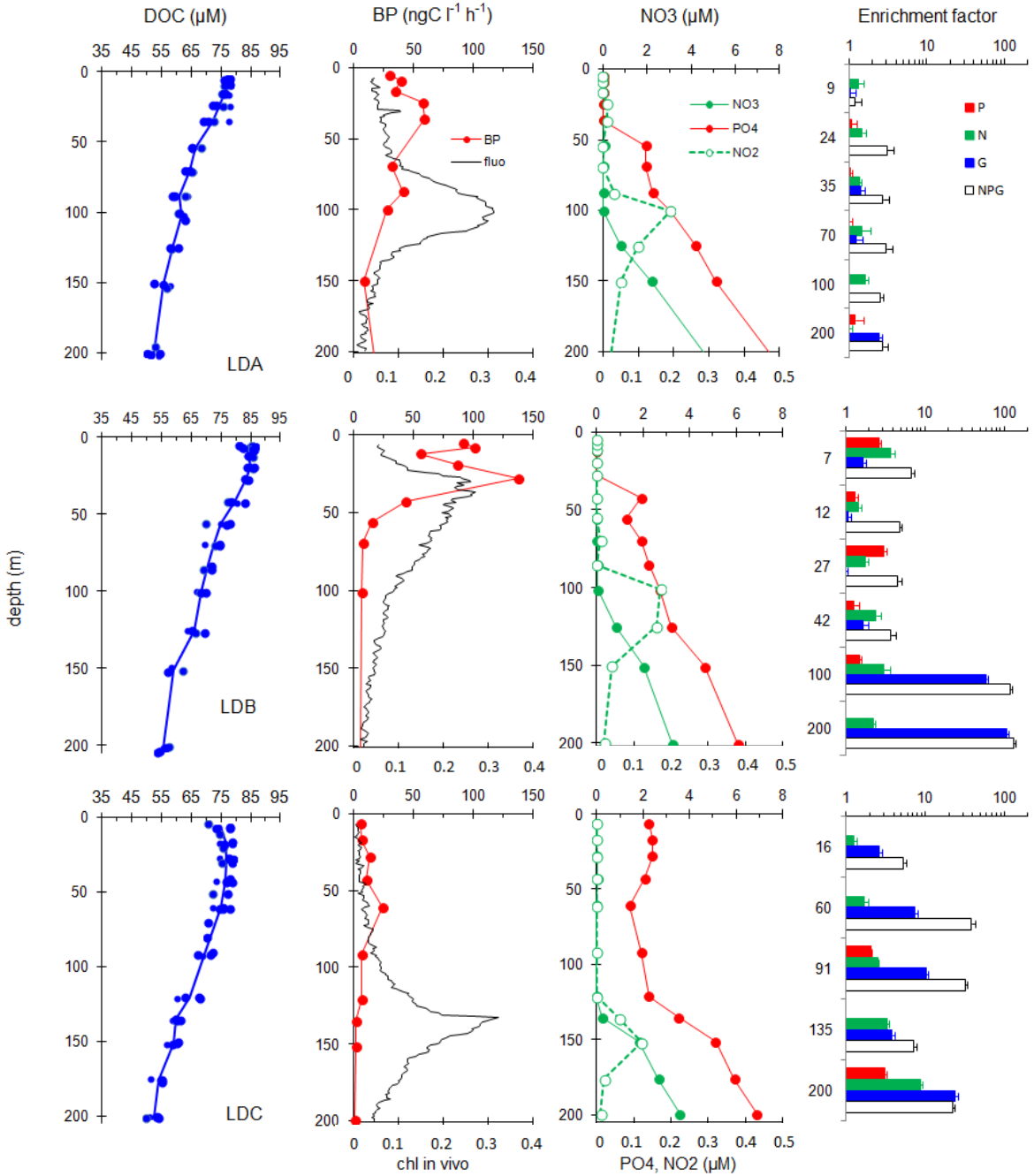

DOC (µM)
BP (ngC l-1 h-1)
NO3 (µM)
Enrichment factor
depth (m)
LDA
LDB
LDC
BP
fluo
NO3
PO4
NO2
P
N
G
NPG
chl in vivo
PO4, NO2 (µM)

Fig 9

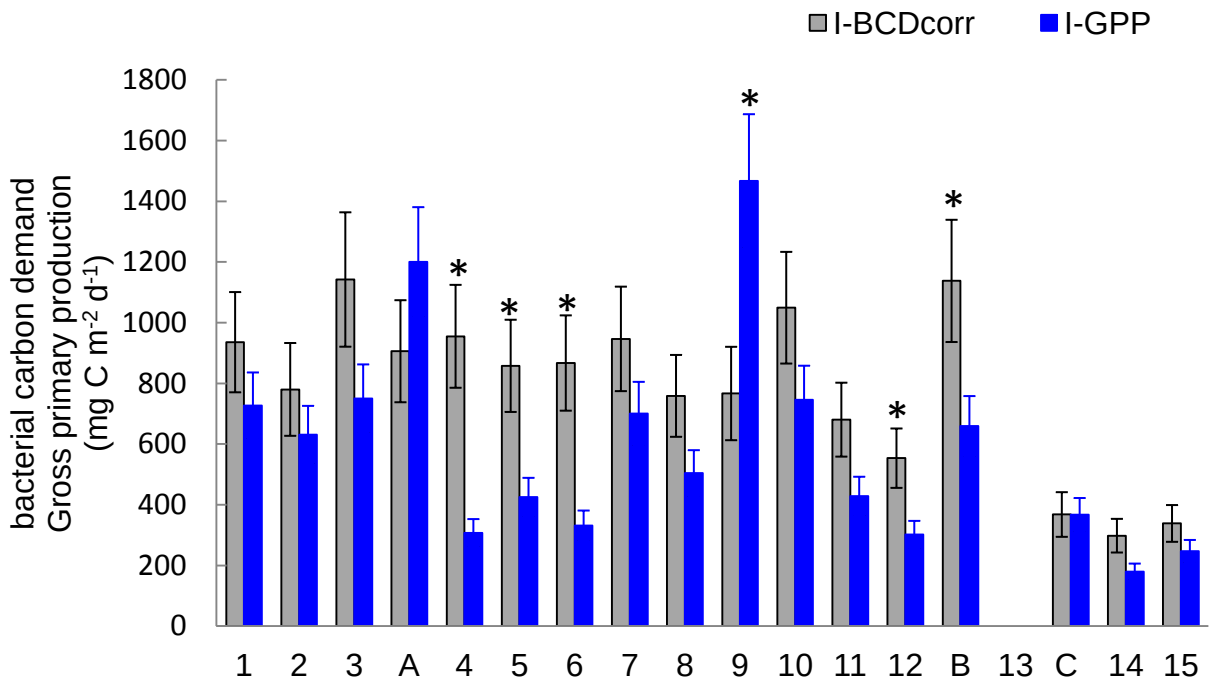

I-BCDcorr
I-GPP
bacterial carbon demand
Gross primary production
(mg C m-2 d-1)
1800
1600
1400
1200
1000
800
600
400
200
0
1
2
3
A
4
5
6
7
8
9
10
11
12
B
13
C
14
15
*

Fig 10

Response to referee 1 M. Aranguren-Gassis

General comments
In the manuscript "Dynamics of phytoplankton and heterotrophic bacterioplankton in the western tropical South Pacific Ocean along a gradient of diversity and activity of diazotrophs", Van Wambeke et al. present estimations of heterotrophic prokaryotic production in the Western Tropical South Pacific region, and they explore the causes of its variability, focusing on autotrophic activity and nutrient availability. The data presented in the paper are very valuable, as the carbon budget in the oligotrophic regions is still a topic of debate, in part because of lack of data to adequately characterize the bacterial contribution to it. The data presented are a great mix of observations and experiments, and the analysis made have great potential. However, the way the paper is written makes the information confusing and the conclusions vague. The title doesn't reflect the contents of the paper, the methods are not complete, the discussion is not well structured or clear, and the conclusions are not in line with the results highlighted in the discussion (See details in specific comments). The English and the writing needs profound review.

We thank Dr. Maria Aranguren-Gassis for her constructive comments. We respond to her below using regular black fonts and provide references to modified text in our manuscript using regular blue fonts. A native English speaker will check the revised version of the ms.

Specific comments
- Title: The authors mention in the title a gradient of diversity and activity of diazotrophs, but such gradient is not shown in the paper. They base part of their discussion in different groups of diazotrophs described during the same cruise by other authors (lines 530-541), but as they described it, it is not a diversity gradient, just differences in the dominant genera. The diazotrophs activity gradient is not clear either in the paper. I would suggest for the title to focus more on the analysis made to elucidate the factors controlling the bacterioplankton activity in different regions of an oligotrophic system.

The title was modified as:
'Dynamics and controls of heterotrophic prokaryotic production in the western tropical South Pacific Ocean: links with diazotrophic and photosynthetic activities.'

- Abstract: The abstract is a good summary of the paper, but I think some parts can be removed:
** Line 28: the i.e. can be removed, it makes the sentence too long, and it is not necessary*
It is done

** Line 30: The BGE estimation doesn't provide useful information here*
We removed this sentence

** Lines 33-36: I don't find this information about the bloom developed along the paper, I think this should be removed from here.*
We agree that the study of a bloom collapse at site LDB did not constitute the main focus of the paper. This part was rephrased and moved up in the abstract.

- Methods: Some variables have a lot of weight in the discussion but methods are not described. For example Nitrogen fixation rates, community respiration and GPP, or nutrients

(nitrate, nitrite, and phosphate) concentrations. At least a brief description of the methods should be included, even if they have been explained somewhere else.

Since the submission of our manuscript, papers devoted to the study of nitrogen fixation rates (Bonnet et al., 2018) and nutrients and organic matter distribution (Moutin et al., 2018) have been published in the OUTPACE special issue, in which detailed methodologies are available. However, to provide guidance to the reader, we added a few sentences describing methodology in M&M section 2.1 as follows:
'Besides measurements of chlorophyll *a*, BP, PP, T_{DIP} and DOC described below, other data presented in this paper include hydrographic properties, nutrients, N_2fix, for which detailed protocols of analysis and considerations for methodology are available in Moutin et al. (2017; 2018) and Bonnet et al. (2018). Briefly, DIP and nitrate concentrations were measured using standard colorimetric procedures on a AA3 AutoAnalyzer (Seal-Analytical). The quantification limits were 0.05 µM for both nutrients. N_2 fixation rates were measured using the $^{15}N_2$ tracer method in 4.5 L polycarbonate bottles inoculated with 5 ml of $^{15}N_2$ gas (99 atom % ^{15}N, Eurisotop). Note that the risk of underestimation by this bubble method was checked by subsampling and fixing 12 ml of each bottle after incubation and analyzing the dissolved $^{15}N_2$ with a Membrane Inlet Mass Spectrometer.'

For O_2 based metabolic rates, since the paper by Lefevre et al. (this issue) is still not submitted, and as Dark Community Respiration are used to estimate bacterial growth efficiency, the protocol has been briefly developed in M&M section 2.5 as follows:
'Rates of dark community respiration (DCR) were used to estimate bacterial growth efficiency (see discussion). Briefly, DCR was estimated from changes in the dissolved oxygen (O_2) concentration during dark incubations of unfiltered seawater (24 h) carried out at LD stations, *in situ* on the same mooring lines used for $PP_{in\ situ}$ (Lefevre et al., this issue). Quadruplicate Biological Oxygen Demand bottles were incubated in the dark at each sampled depth. The concentration of oxygen was determined by Winkler titration. DCR was calculated as the difference between initial and final O_2 concentrations, and the mean standard error of volumetric DCR rates was 0.28 µmol O_2 dm^{-3} d^{-1}.'
In addition, data on integrated DCR rates were added in Table 2.

- Lines 109-112: The criteria used for stations selections is not stated. Even if it is described in other papers, a better explanation should be included here because it can affect the interpretation of the results.

The end of Results 3.1 section was modified as follows:
'The transition between the MA and WGY areas is particularly evidenced by an enhanced degree of oligotrophy in the WGY area. WGY area was characterized by dcm depths deeper than 115 m (Table 2), deep nitracline (130 m) and nitrite peaks around 150 m and detectable amounts of phosphate at the surface (> 100 nM, Moutin et al., 2018). A detailed analysis of the vertical distribution of nutrients and organic matter made it possible to identify two groups of stations within the MA area, each having common biogeochemical characteristics: one group between 160 and 170°E called WMA for 'Western Melanesian Archipelago' clustered SD1, 2, 3 and LDA and a second group South of Fidji called EMA for 'Eastern Melanesian Archipelago' clustered SD6, 7, 9 and 10 (Moutin et al., 2018). Main biogeochemical differences between these two groups of stations were related to shallower depths for phosphacline (20m), nitracline (76m), dcm (82 m), in WMA group (see Table 2 and Figure 5 b, c in Moutin et al., 2018). The EMA group had intermediate depths for these parameters in comparison to WMA and WGY, (phosphacline 44 m, nitracline 100 m and dcm 105 m).

Although geographically included within the MA area, LDB corresponded to a particular bloom condition and is therefore presented and discussed separately.'

- *Line 113: It should be mention here that the sampling in LD stations was Lagrangian.*
This has been done

- *Lines 151 and 161: The word "occasionally" is too vague, please specify at least how many times.*
This has been done (9 times for time kinetics, 5 times for concentration kinetics)

- *Lines 165-179: The incubation time used should be specified.*
This has been done as follows:
'Incubations times lasted 4 (western stations) to 24h (south Pacific Gyre area) and were chosen according to expected T_{DIP}.'

- *Lines 185 and 207: Are the cast numbers necessary? I think they can be removed.*
Yes, they have been removed

- *Line 230: The authors talk about a gradient, but they don't specify what kind of gradient. A gradient of productivity? A gradient of diazotrophs activity?*
To improve clarity, we changed the first sentence of paragraph 3.1 as follows:
'The longitudinal transect started North West of New Caledonia, crossed the Vanuatu and Fidji Arcs and finished inside the western part of the ultra-oligotrophic South Pacific Gyre.'

- *Lines 240-245: Authors say that nutrients and organic matter distribution allowed them to distinguish two regions, but those data are not shown in the paper. At least, a description of the differences between the regions should be included. For example, you can include some extra data in Table 2 with nutrients and organic matter concentration, or whichever criteria used to identify those two regions.*
See previous response describing the modification of the end of section 3.1

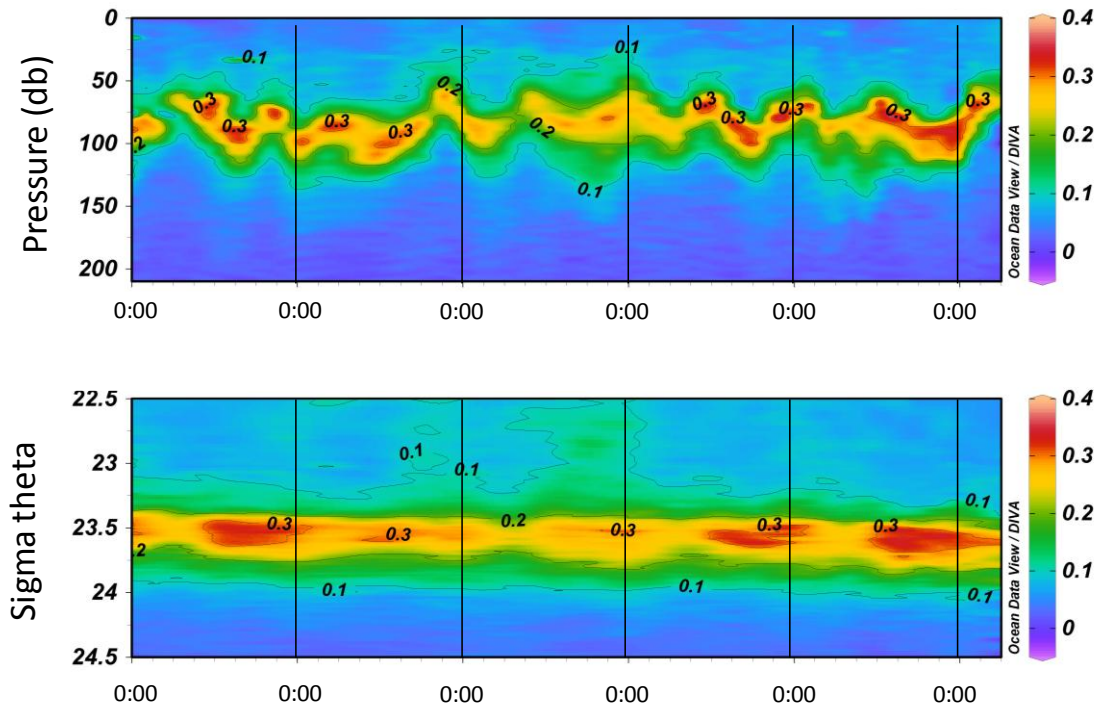
- *Lines 236-246 are confusing and need to be rewritten.*
See previous response describing the modification of the end of section 3.1

- *Line 249: "Averaged per SD station, the dcm fluctuated..." I don't understand what that means and what the following ranges refer to.*
We think that the misunderstanding comes from our definition of dcm: in the ms introduction, we defined 'dcm' as 'the depth of the deep chlorophyll maximum' (see line 48 of the first version) instead of the more common use of this acronym as the 'deep chlorophyll maximum'. In the revised version, we changed that definition as follows:
'The South Pacific gyre (GY) is ultra-oligotrophic, and is characterized by deep UV penetration, by deep chlorophyll maximum (dcm) depth down to 200 m, and by a 0.1 µM nitrate (NO3) isocline near 160 m (Claustre et al., 2008b; Halm et al., 2012)'
When necessary, we added the word 'depth' after dcm, to help the reader understand that the descriptions of LD site variability with time refer to the vertical change of the dcm depth.

- *Line 269: I suppose what authors meant is that TDIP increased with depth, not the vertical profiles themselves.*
Yes of course, this has been corrected.

- Line 281: I don't think the periodicity of the dcm fluctuation is evident in figure 5. That fluctuation and the increase of fluorescence in the afternoon are not well described. Those patterns are not apparent in the figures, and not statistical analysis is presented. However, I think those results can be avoided because authors don't mention them along the discussion at any point.

We recognize that such patterns are much more visible when plotting fluorescence versus density instead of depth. See for example what it would give for site LDA:



We agree partly with the referee's recommendations. The part focusing on the increase of fluorescence in the afternoon which is not developed in the discussion has been deleted. However, the part describing internal waves, particularly on site LDA, is important because such temporal variability makes difficult to compare profiles of biogeochemical parameters or biological fluxes when they were not made at the same time. Thus, this part was kept.

-Line 286: Values from In situ and on deck incubation cannot be directly compared, as temperatures for the incubations are different. Particularly for samples from depths below the mixer layer. So authors shouldn't highlight a higher value from on deck incubations without a proper analysis of correspondence between on deck and in situ estimations.

A new paragraph was added at the beginning of section 3.4 as follows:

'There are several limitations with comparing PP_{deck} and $PP_{in\ situ}$. Incubation on mooring lines for 24h dawn-to-dawn is considered to be a good compromise by JGOFS recommendations (JGOFS, 1988), as temperature and light are close to *in situ* conditions (except UV). Incubation on deck, under simulated *in situ* conditions suffers from biases related to the use of artificial screens to mimic light attenuation with depth, and also from biases related to temperature decrease for deeper samples, as they are incubated at sea-surface temperature. During our cruise, at each LD site on day 5, we used both incubation methods, and did not

sample the same CTD cast: $PP_{in\ situ}$ was sampled at 3:00 AM while PP_{deck} was sampled at 9:00 AM. At site LDA, differences between the mean $IPP_{in\ situ}$ and IPP_{deck} were particularly high. Besides artifacts related to light and temperature described above, one of the explanation could be due partly to internal waves (de Verneil et al., 2017; Bouruet-Aubertot et al., this issue) as for instance the dcm depth changed from 69 m to 87 m between the 3:00 ctd cast and the 9:00 ctd cast at the site LDA on day 5. At the site LDB, the bloom collapsed rapidly and a trend with time was clearly detected, making the comparison between both methods impossible, even with only a time lag of 6h. For this reason, and to keep relative comparisons consistent, we used only PP_{deck} data when exploring relationships between BP, PP, N_2fix and T_{DIP}.'

de Verneil, A., Rousselet, L., Doglioli, A. M., Petrenko, A. A., Maes, C., Bouruet-Aubertot, P., and Moutin, T.: OUTPACE long duration stations: physical variability, context of biogeochemical sampling, and evaluation of sampling strategy, Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-455, in review, 2017

Bouruet-Aubertot, P., Cuypers, Y., Le Goff, H., Rougier, G., Picheral, M., Doglioli, A., Yohia, C., de Verneil, A., C ffin, M., Petrenko A., Lefevre, D., Moutin, T. Longitudinal contrast in Turbulence along a 19S section in the Pacific and its consequences on biogeochemical fluxes. Biogeosciences Discuss., this issue, in prep.

We checked that both types of rates were not mixed in any of our interpretations: Time variability on sites LDA, LDB and LDC only used $PP_{in\ situ}$ (Figs 5, 6, 7), whereas analysis of longitudinal trends, and correlations with BP only included PP_{deck} data (Figs 2, 3, 8 and 10). Because in the first version of the manuscript, the correlations described on Fig 8 included both types of rates, we now have done the analysis including only PP_{deck} data. This is why values cited on equation linking BP with PP have been slightly changed in the revised version (see below), but the conclusions did not change.

-Lines 324-326: Figure 8 shows a linear regression analysis, but in the text, authors present the correlation coefficient (r), but not in the figure or in the text they mention the significance of the fitting. With the correlation coefficient, authors shouldn't interpret the results as a dependency, because the correlation between two data sets doesn't indicate causality of one of the variables from the other.

We added p in the equations:

log BP=0.842 log PP - 0.57, n=47, r = 0.26, p=0.04 and
log BP=0.808 log PP - 0.53, n=90, r = 0.67, $p < 0.001$

for samples where T_{DIP} was $\leq$ 100 h and > 100 h, respectively

log BP=0.752 log N_2fix - 0.78, n=39, r = 0.52, $p < 0.001$ and
log BP=0.438 log N_2fix - 0.31, n=55, r = 0.43, $p < 0.001$

for samples where T_{DIP} was $\leq$ 100 h and > 100 h, respectively

- Line 331-334: Those N2fix temporal trends are not shown anywhere. If authors don't want to show them in a figure, use some statistics to state those patterns.

To better illustrate the longitudinal variability, we modified Fig. 3b and plotted integrated N_2fix rates, as well as the N_2fix rates to bacterial nitrogen demand ratio instead of the bacterial nitrogen demand. The new Fig. 3 can be found at the end of the responses to the reviewer's comments.
N_2fix temporal trend and the concomitant changes in the ratio of N_2fix to bacterial nitrogen demand at site LDB was explicitly detailed and we added statistic results for comparison of this ratio between site LDA and site LDC.

- Line 393-404: The definition of the regions is not well described. Some suggestions:
** Use the same terms to name them along the entire manuscript.*
In the revised version of our manuscript, we paid attention to use the terms WMA (Western Melanesian Archipelago), EMA (eastern Melanesian Archipelago) and WGY (western part of the South Pacific Gyre) when they were cited all along the ms.

** Show them on the map (figure 1)*
We modified Figure 1 that can be seen at the end of the responses to the reviewer's comments.

** Refer here to Table 2, and complete the table with the criteria described here (nitracline depth).*
Distinction between WMA, EMA and WGY group of stations is based, among other parameters, on dcm depth which is already included in Table 2. Biogeochemical characteristics explaining differences between WMA, EMA and WGY stations are based on differences between depths of phosphacline, nitracline and dcm, which more or less followed the same trend, i.e. intermediary depths for EMA stations (between WMA stations, shallower, and WGY stations, deeper). Depth of nitracline and phosphacline are indicated in Table 2 of Moutin et al (2018) and depth of phosphacline was added for WMA and EMA in Figure 4. Hence, we think it is unnecessary to add nitracline and phosphacline depths in Table 2.

** Define what "distinct nutrient distributions" means or show it in a plot*
See previous response describing the modification of the end of section 3.1. Sentences describing dcm, nitracline and phosphacline depths are not anymore used in section 4.1

** In figure 4 put in different colors or patterns the profiles for each region*

The new version of Fig. 4 is presented at the end of the responses to the reviewer's comments.

- Line 422: "after filtration and removal... producers" corresponds to methods section.

This part of the sentence was removed

- Line 431-432: Why is the information in the last sentence of this paragraph relevant? Please, elaborate

The last sentence was moved upper in this paragraph in a more appropriate place. So that the paragraph is now organized as follows:
'Bacterial growth efficiencies (BGE) obtained from biodegradation experiments ranged 6–12 %, with a small labile fraction of DOC (only 2–5 % of biodegradable DOC in 10 days). Thus, the bulk DOC was mainly refractory, although DOC concentration was higher in surface waters (Moutin et al., 2018). Large stocks of DOC, with C/N ratio ranging 16 to 23 have also

been reported in the surface waters of the SPG (Raimbault et al., 2008). Both high C/N ratios and a small labile fraction suggests that this surface bulk pool of DOC is probably largely recalcitrant due to UV photodegradation or photooxidation (Keil and Kirchman, 1994; Tranvik and Stephan, 1998; Carlson and Hansel, 2015) or by action of the microbial carbon pump (Jiao et al., 2010). Small BGE and small labile fraction could also be due to strong resource dependence as low nutrient concentrations cause low primary production rates, and low transfer across food webs. Indeed, Letscher et al. (2015) also observed surface DOC recalcitrant to remineralization in the oligotrophic part of the eastern tropical south Pacific. But as shown by these authors, incubation with microbial communities from the twilight zone, provided by addition of an inoculum concentrated in a small volume, allowed DOC remineralization. This was explained by relief from micronutrient limitation or potential role for co-metabolism of relatively labile DOC provided by the inoculum with more recalcitrant DOC. Our enrichment experiments effectively suggest nutrient limitation, although the second hypothesis could not be excluded.
In order to better explain the variability of BGE measurements, we also estimated this parameter indirectly, using dark community respiration (DCR) and BP data that were measured simultaneously. We converted DCR to carbon units assuming a respiratory quotient RQ = 0.9, and computed BGE from Ze-integrated BP and DCR assuming either bacterial respiration (BR) to be within a range of 30 % of DCR (BGE=BP/(BP+DCR*0.9*30 %), Rivkin and Legendre, 2001; del Giorgio and Duarte, 2002) or 80 % of DCR (BGE=BP/(BP+DCR*0.9*80 %), Lemée et al., 2002; Aranguren-Gassis et al., 2012). The range of these indirect estimates of BGE were similar to those obtained from the biodegradation experiments: 3–12 % at site LDA, 4–17 % at site LDB and 2–7 % at site LDC. Note, however, an increasing trend from day 1 to day 5 at site LDB: on average 8 % on day 1, 10 % on day 3 and 12 % on day 5. Including all direct and indirect estimates, the mean (± sd) BGE was 8 ± 4 % (n = 21).

- *Lines 445-462: This paragraph is not well linked to the rest of the discussion. There is not any mention of the present paper results, and it is not clear the contribution of the present paper to the debate described in the paragraph. Please, elaborate.*

We completely re-organized section 4.2: We now start by the paragraph discussing metabolic balance. Then, the paragraph introducing PP and GPP was modified as follows:
'It is known that the in vitro ^{14}C method measures an intermediate state between net PP and GPP. However, Moutin et al. (1999) showed that GPP could be reasonably estimated from daily net PP determined from dusk-to-dusk as: GPP = 1.72 * PP, a ratio also used by others authors (Loisel et al., 2011). On the other hand, dealing with the assumptions made to convert hourly leucine incorporation rates to daily BCD, there are many biases that have been largely debated, including mostly those resulting from daily variability, assumptions on BGE or BR (Alonzo-Saez et al., 2007; Aranguren-Gassis et al., 2012b), carbon to leucine conversion factors (Alonso-Saez et al., 2010), and light conditions of incubations including UV (Ruiz-Gonzales et al., 2013). For this cruise, we measured data to discuss BGE variability. Daily variability is also taken into account using results from previous experiments in the South Pacific Gyre (BIOSOPE cruise, Van Wambeke et al., 2008). Finally, we also discuss one largely unexplored bias, related to the ability of *Prochlorococcus* to assimilate leucine in the dark.'

Loisel, H., Vantrepotte, V., Norkvist, K., Mériaux, X., Kheireddine, M., Ras, J., Pujo-Pay, M., Combet, Y., Leblanc, K., Dall'Olmo, G., Mauriac, R., Dessailly, D., and Moutin, T. : Characterization of the bio-optical anomaly and diurnal variability of particulate matter, as

seen from scattering and backscattering coefficients, in ultra-oligotrophic eddies of the Mediterranean Sea, Biogeosciences, 8, 3295-3317, doi:10.5194/bg-8-3295-2011, 2011

Then, we followed by 3 paragraphs describing successively BGE variability, daily variability and finally the correction factors linked to the assimilation of leucine by *Prochlorococcus*. The short paragraph on daily variability as requested by the second referee:
'Bias introduced when converting hourly to daily BP rates was not studied here, but we use a dataset obtained in the South Pacific Gyre (Van Wambeke et al., 2008) to estimate conversion errors. During the BIOSOPE cruise, vertical profiles of BP were acquired using the leucine technique along the euphotic zone, every 3 h up to 72 h, at three selected sites using Lagrangian sampling strategy. For the 3 series of profiles, standard deviations of IBP with time were 13 % (n = 13), 16% (n = 16) and 19 % (n = 9). Thus, standard errors represented 3.6, 4.2 and 6.1 % of the mean BPI, respectively. We used the average value of this percentage (5 %) to estimate the bias introduced by the conversion from hourly to daily IBP estimates of the OUPACE cruise. '

- *Lines 482-488: This paragraph is confusing and needs rewriting*

The paragraph was corrected as follows:
'Using flow cytometry cell sorting of samples labelled with ^{3}H-leucine during the OUTPACE cruise, Duhamel et al. (in revision) demonstrated the mixotrophic capacity of *Prochloroccoccus*, as this phytoplankton group was able to incorporate leucine, even under dark conditions, albeit at lower rates than under light conditions. This group was found to be able to assimilate ATP, leucine, methionine as well as glucose, a single C-containing molecule (Duhamel et al., in revision, and ref therein). To date, few organic molecules have been tested and mainly those including N, P or S sources. As leucine assimilation by *Prochloroccoccus* was significantly detected in dark incubations in all examined samples, it will affect BP measurements. We thus corrected (BP_{corr}) to represent the assimilation of leucine in the dark by heterotrophic bacteria alone. Based on Duhamel et al. (in revision), leucine assimilation by HNA+LNA bacteria in the dark corresponded on average (± sd) to 76 ± 21 % (n = 5, range 44–100 %) of the activity determined for the community including *Prochlorococcus* (HNA + LNA + Proc).'

- *Lines 490-492: I don't understand the calculations described in here*

We changed Fig. 10, presenting BCD_{corr} instead of $BP_{corr,}$ so that GPP and bacterial carbon demand could be directly compared.

- *Lines 490-500: What is the overall contribution of all these calculations to the paper?*

The originality is that we compiled the influence of cumulated biases affecting GPP, BCD and their ratio by considering the propagation of errors related to the variability of the reproducibility of measurements, daily variability, BGE variability, and the *Prochlorococcus* assimilation of leucine.

- *Lines 506-509: I don't see the relation between the three first lines of the paragraph and the following ones.*

The first sentence has been moved later in this paragraph when we talk about N and C limitation in WGY area. The second sentence has been removed.

- *Lines 548-549: I think it is incorrect to deduce competition ability from this correlation*

We removed this term. This paragraph has been modified as follows:
We found that the slope of the regression between N_2fix rate and BP was greater and the correlation was better within the mixed layers and when the T_{DIP} is low (<100 h), i.e. in areas characterized by low phosphate availability (Moutin et al., 2008), whereas in this waters variability of PP explained slightly the vaiability of BP (r=0.26). A better correlation between BP and N_2fix than between BP and PP, would suggest that bacteria may have been more dependent on the availability of a new N source than a new C source, which is in agreement with results from enrichments at LDA and LDB. Because T_{DIP} was lower in areas of high N_2fix rates, it is likely that DIP drawdown was due to diazotrophs, which while bringing new sources of N, reduced DIP availability. Indeed, at the site LDB within the mixed layers, BP increased after N addition alone but also after P addition alone, which suggests a direct limitation of BP by N and potentially a cascade effect of P addition towards heterotrophic prokaryotes : P would directly stimulate N_2 fixers which rapidly would transfer new N and labile C available to stimulate BP'

- *Conclusions: The conclusions don't reflect the discussion or even the results presented*

From line 584, the end of the conclusion was modified as follows:
'Our results provide a unique set of simultaneous measurements of BP, PP and N_2fix rates in the WTSP. BP obtained in the WTSP was in the same range as those previously measured in the GY area eastern of 140°W. BGE was low and the bulk DOC was found to be mainly refractory. In surface, nitrogen and relatively DIP depleted waters, BP was more strongly correlated to N_2fix than to PP, while the more traditional coupling of BP with PP occurred deeper in the euphotic zone. This suggests that in the surface layers with greater diazotrophic activity, BP was more dependent on the availability of new N from N_2 fixers than on the availability of fresh C from primary producers, which was also demonstrated through enrichment experiments. We showed that the interpretation of PP and BP fluxes based on instantaneous methods (radioisotopic labelling) needs regular tests to verify the major methodological biases and conversion factors hypotheses. In particular, to make conclusions about the metabolic state of oceanic regions, it is necessary to consider the variability of all conversion factors used to estimate carbon-based GPP and BCD. In addition, the use of the leucine technique to estimate BP should be used with caution in N-limited environments due to the potential mixotrophy by cyanobacteria.'

- *References: There are six not published references in the list, and some of them have data with a lot of weight in the discussion.*

This is inevitably a problem during the editing process of special issues. Among the 6 publications not published in December 2017, three of them are now in Biogeosciences Discussions and one has been published in Applied Microbial Ecology:

Bonnet, S., Caffin M., Berthelot H., Grosso, O., Benavides, M., Helias-Nuninge, H., Guieu, C., Stenegren, M. and Foster, R.: In depth characterization of diazotroph activity across the Western Tropical South Pacific hot spot of N_2 fixation, Biogeosciences Discuss., doi.org/10.5194/bg-2017-567, 2018

Dupouy, C., Frouin, R., Tedetti, M , Maillard, M.., Rodier, M., Lombard, F., Guidi, L., Picheral, M., Duhamel, S., Charrière, B., and Sempéré, R.: diazotrophic *Trichodesmium* influences ocean color and pigment composition in the South West tropical Pacific, Biogeosciences Discuss., doi.org/10.5194/bg-2017-570, in review, 2018

Moutin, T., Wagener, T., Caffin, M., Fumenia, A., Gimenez, A., Baklouti, M., Bouruet-Aubertot, P., Pujo-Pay, M., Leblanc, K., Lefevre, M., Helias Nunige, S., Leblond, N., Grosso, O. and de Verneil, A.: Nutrient availability and the ultimate control of the biological carbon pump in the Western Tropical South Pacific Ocean. Biogeosciences Discuss., /doi.org/10.5194/bg-2017-565, 2018.

Tenorio, M., Dupouy C., Rodier, M., and Neveux, J. Filamentous cyanobacteria and picoplankton in the South Western Tropical Pacific Ocean (Loyalty Channel, Melanesian Archipelago) during an El Nino episode, Appl. Microb. Ecol., doi.org/10.3354/ame01873, 2018

- *Table 1: Better put the PP units on the table. It would be really helpful to group the rows by region, so it is easier to follow the description in Lines 403-415.*
These 2 recommendations have been followed.

- *Figure 1: a more general map to locate the cruise area would be useful. In the legend, the fourth line will be easier to read using "respectively".*
The legend has been modified as suggested. We changed Figure 1 and Nouméa and Papeete are now indicated to help for localization, letters and numbers of stations are more contrasted, and we added colored squares to identify the groups of stations corresponding to WMA, EMA and WGY areas. The new Fig 1 is presented at the end of this author comment

- *Figure 2: I suggest using the same units for the two panels to make them directly comparable. Put stations number in both plots.*
We added station numbers in both plots. We found unnecessary to use the same units as the goal of such plots is just to illustrate trends. Scientists working with bacterial production data are more familiar with hourly units, closer to what has been really measured. Comparison is however possible on Figure 8a (volumetric rates), 2 and 10 (integrated rates) where the same units are used for PP (GPP) and BP (BCD) rates.

- *Figure 3: * The units on the panel B are incorrect, it is mmol.*
This has been corrected
** Why are data at station 13 missing? I don't find the explanation.*
The explanation was on the legend of Table 2. We added the sentence also on Figure 3.
** As I understand, the bars on figure 3 represents the values of each variable in every station, so these plots are not histograms, they are bar charts.*
Yes, the Legend has been modified
** Bars should be represented by the corresponding error bars.*
We added error bars (standard errors)

-*Figure 4: this figure needs to be improved. Some suggestions:*
** Make the station names consistent with other figures.*
This has been done
** Group the profiles by region, with color or pattern, or make 3 panels, one for each region.*

** Talking about this figure in the text (line 269) authors use the phosphacline. Represent the phosphacline here to help.*
Fig. 4 has been modified and now includes 4 panels with plots separating EMA, WMA and EGY stations. The depth of phosphacline was added. The new Fig. 4 is presented at the end of the responses to the reviewer's comment.
** I would incorporate the profiles for the Long stations in figure 9, as you use the information in the discussion of the experiments.*
T_{DIP} vertical profiles at sites LDA, LDB and LDC were done only once per LD station, on day 5 and not on day 2 when other parameters presented in Figure 9 were measured. As we explained in the ms, due to the high internal waves at site LDA, as well as the bloom collapse at site LDB, there was too much variability between day 2 and day 5 at LD stations and therefore, we preferred not to insert T_{DIP} data on Figure 2.

- Figures 5, 6 and 7:
** Vertical axis in the second panel should say fluorescence instead of chl, as you explain in the text (e.g., line 280*)
This has been corrected

** When describing these figures in the text, you use the density. Including the density level lines in the figures will be a good idea.*
Yes it is. We modified the Figure accordingly. For example the new Fig. 5 is presented at the end of the responses to the reviewer's comment.

** Explain in the legend what the vertical lines in the second panel mean, and make them the same color than the profiles in the third panel.*

We added a sentence in the legend:
'On the in vivo fluorescence graph, vertical bars show the 12:00 AM ctd cast sampled for BP each day (1 to 5) with corresponding colours used for plotting BP vertical profiles'.
In fact, the color code was already done. We now use thicker lines to better see the differences.

- Figure 10: What is it that you represent in here is not clear for me, not in the text or the figure legend. Please make the description of the calculation more clear and explain better the meaning and the interpretation. Use station names consistent with the rest of the paper.
This has been modified, in the text as well as in the legend. We also modified the figure, plotting bacterial carbon demand instead of BP. A copy of the new Fig. 10 can be found at the end of the responses to the reviewer's comments.

Technical corrections
– Line 23: space is missing between With and N2 loom
– Lines 94 and 97, the period is missing
- Lines 110 and, the first n in Lagrangian is missing
- Line 119: I think authors meant experiments (in plural)
- Line 234: a bracket is missing before the references
All five corrections done

- Lines 236-246 are confusing and need to be rewritten.
See above the modification of the end of section 3.1

- *Line 249: "Averaged per SD station, the dcm fluctuated..." I don't understand what that means and what the following ranges refer to.*
See response above (dcm versus dcm depth)

- *Line 269: Vertical profiles cannot increase or decrease with depth, I assume you are talking here about TDIP decreasing with depth. Please rewrite.*
Yes sorry, this has been corrected

- *Line 278: Please, check this sentence. Space is missing between down and in. "Comumn" I suppose means columns with l. There is a comma instead of a period after the bracket. The sentence doesn't make sense in general.*
The sentence was modified as follows:
'Site LDA presented variable dcm depth over time (63 to 101 m, Table 2), as illustrated by patches of in vivo fluorescence moving up and down the water column with time, along a band of 40 m height (Fig. 5). However, the dcm depth corresponded to a stable density horizon (σt 23.55 ± 0.04 kg m^{-3}), and thus this fluctuation in dcm depth corresponded to internal waves characterized by a periodicity of about 2 per day (Fig. 5).'

- *Line 287: delete the bracket before IPPDECK*
Done

- *Line 327: PP instead of BP - Line 345: Those abundances, I guess are bacterial abundances*
This has been corrected. We now only use BP data and DOC data in biodegradation experiments

- *Line 346: a decimal point is missing in 014*
- *Line 347: the lowest instead of the lowerest instead of the lower*
The 2 corrections were done

New versions some Figures.

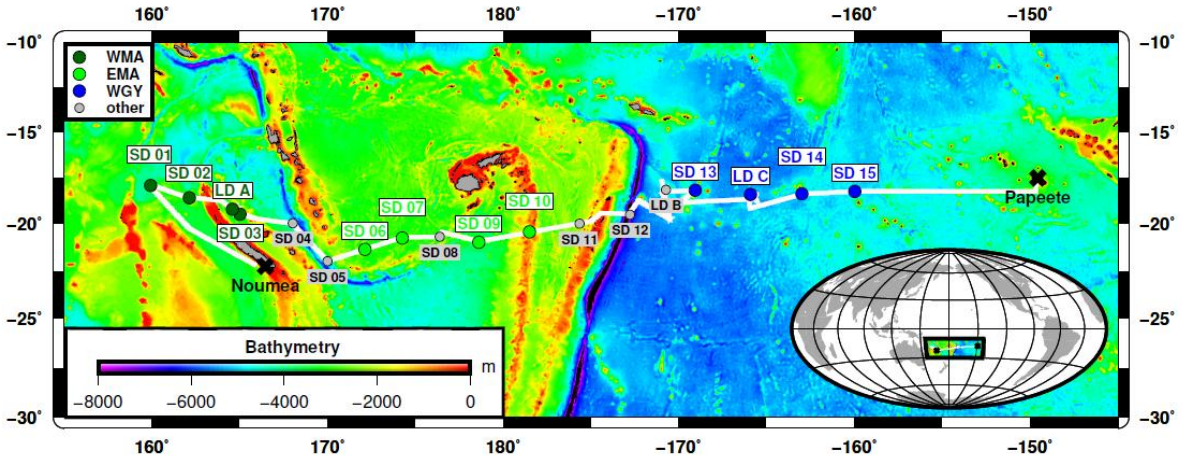


Figure 1 Stations locations during the OUTPACE cruise. The white line shows the ship track (data from the hull-mounted ADCP positioning system). In dark green WMA (western Melanesian Archipelago) included SD1, 2, 3 and LDA; in light green, EMA: eastern Melanesian Archipelago included SD 6, 7, 9 and 10 and in blue WGY (western gyre) included stations SD13, 14, 15 and LDC.
Figure courtesy of T Wagener.

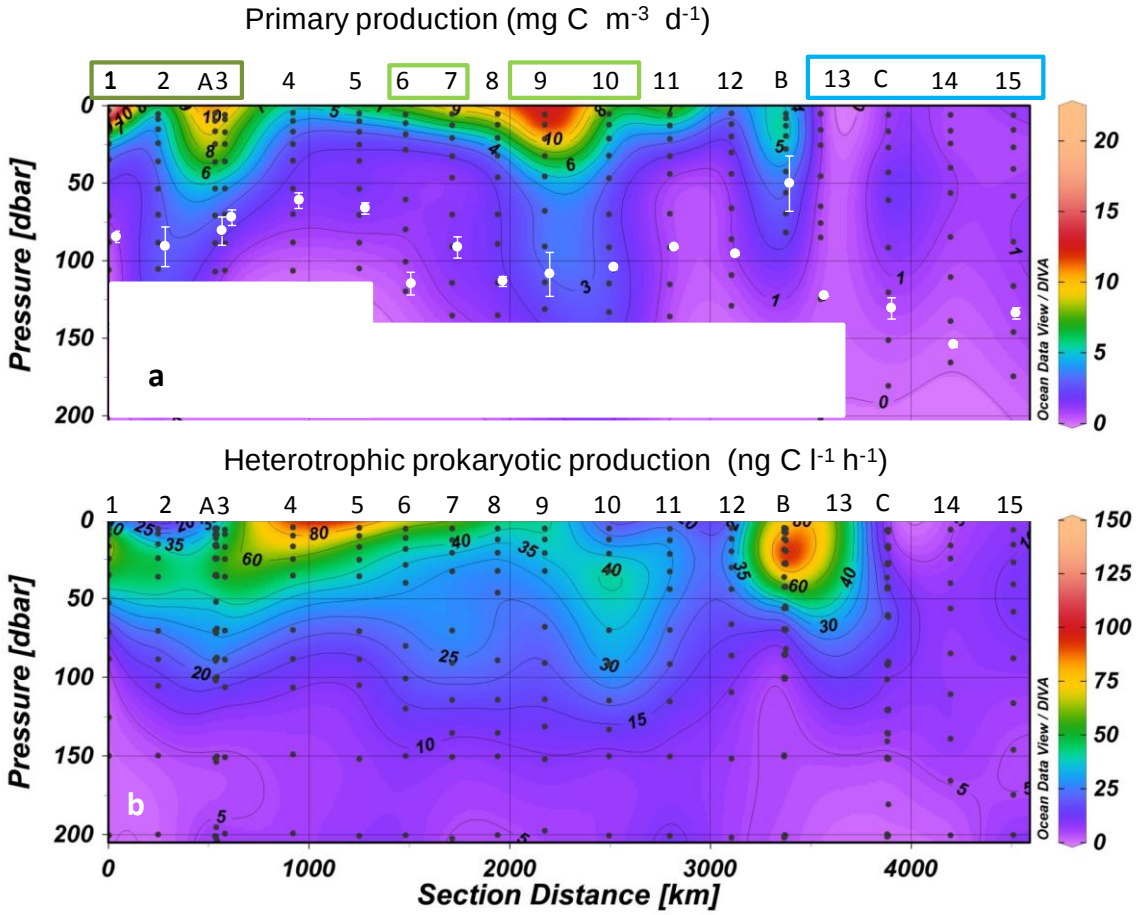


Figure 2 Distribution of primary production (a) and heterotrophic prokaryotic production (b) along the OUTPACE cruise transect. Interpolation between sampling points in contour plots was made with the Ocean Data View software (VG gridding algorithm, Schlitzer, 2004). The white dots in (a) correspond to the average ± sd of the dcm depth at each station. The white rectangles mask abnormal extrapolation due to the absence of PP data.

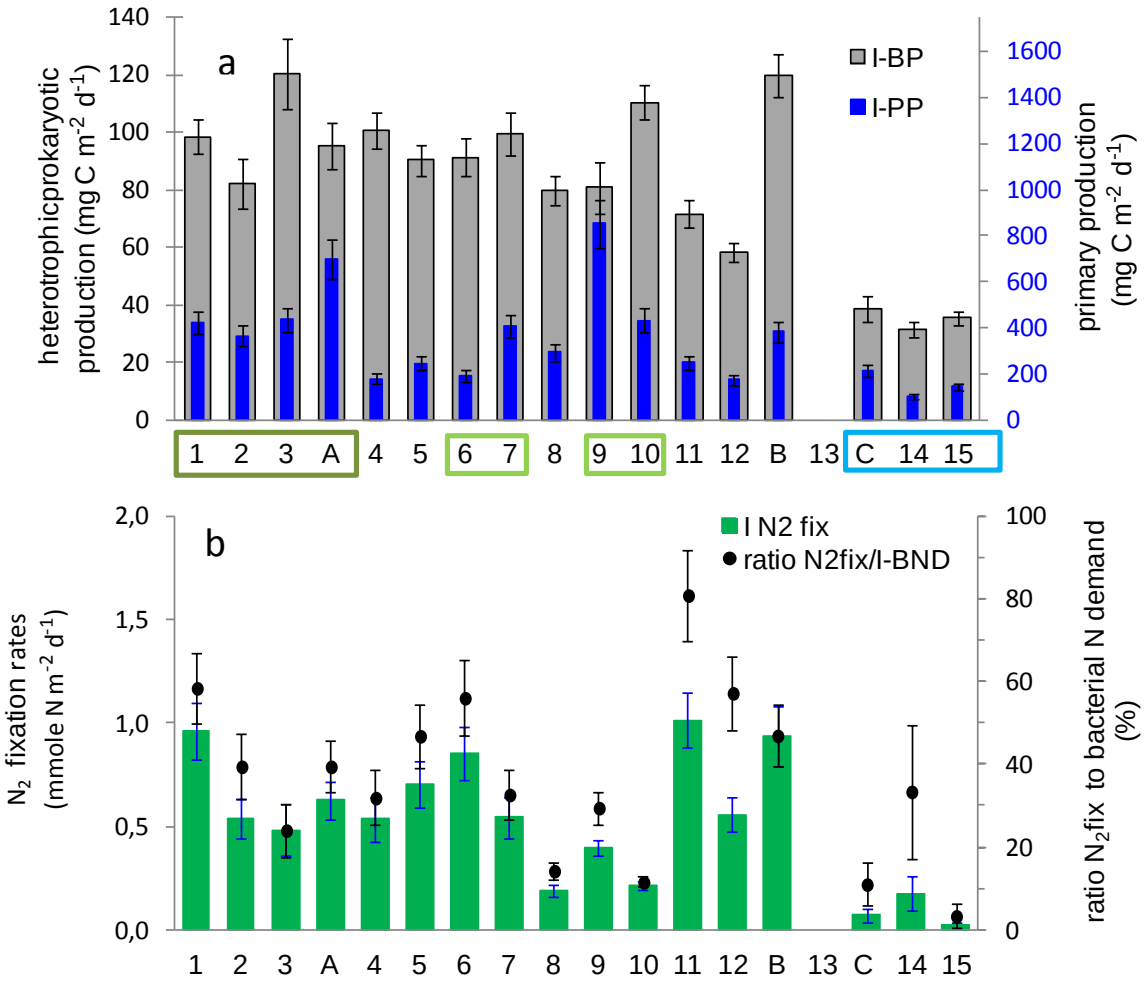


Figure 3 a) Distribution of integrated heterotrophic prokaryotic production (IBP) and primary production (IPP_{deck}) along the transect, data were integrated over the euphotic zone. b) Distribution of integrated N_2 fixation rates and of ratio N_2 fixation rates to bacterial nitrogen demand (I N2fix/I-BND, assuming a bacterial C/N ratio of 5 and no nitrogen excretion) along the transect. Data were integrated down to the deepest sampled depth for N_2 fixation rates. Data plotted for sites LDA, LDB and LDC correspond to BP, PP_{deck} and N_2fix measured on day 5. Error bars are standard errors (s.e.) derived from triplicate measurements at each depth (BP, PP_{deck}, N_2fix rates). For BP, error bars also take into account the daily variability, and final s.e. were calculated after propagation of errors. PP obtained at SD13 was abnormally low (55 mg C m^{-2} d^{-1}) and was excluded; BP and N_2fix rates were not measured at this station.
.

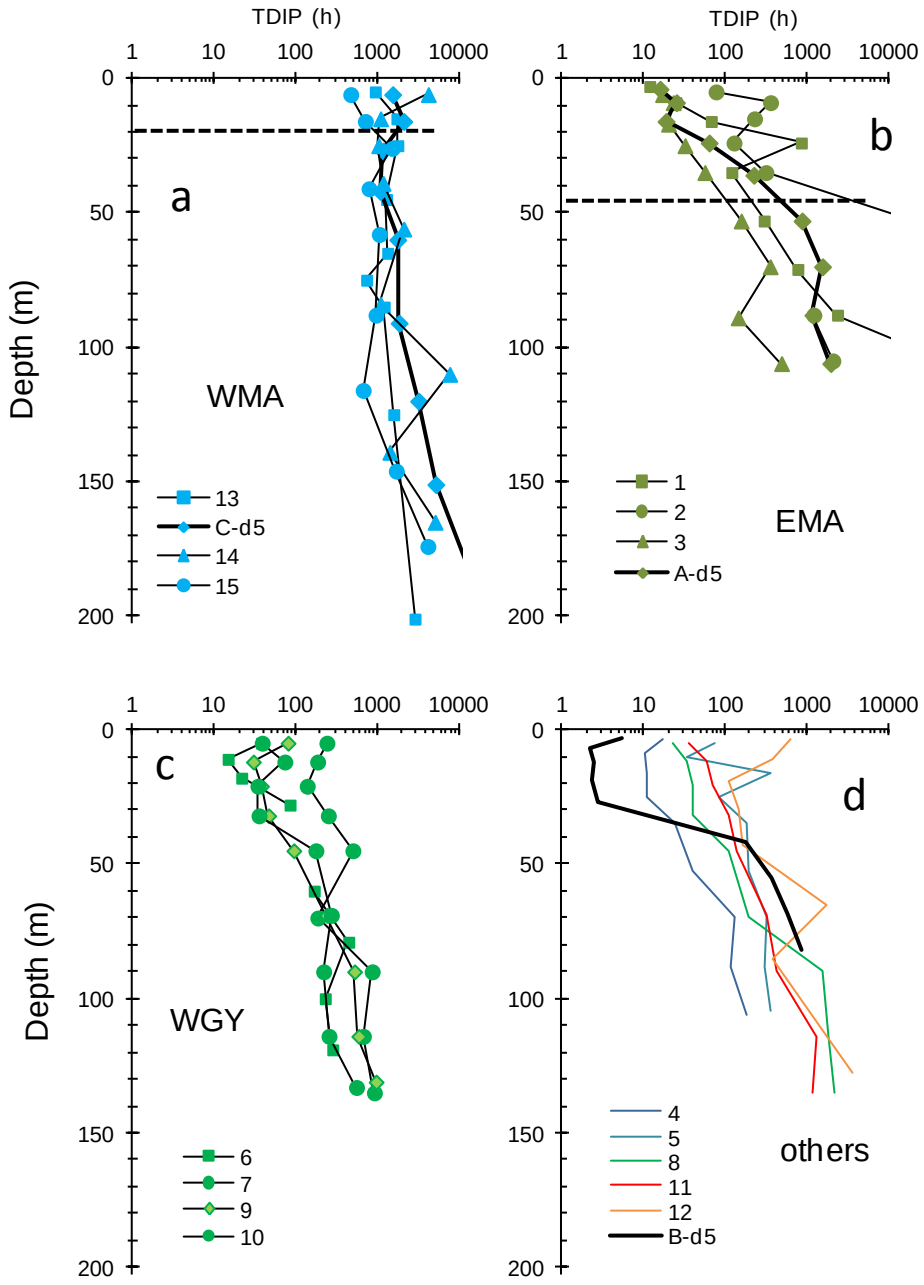


Figure 4 Vertical distributions of phosphate turnover times (T_{DIP}) in groups of stations WMA (a), EMA (b), WGY (c) and other stations (d). At the long-duration stations LDA, LDB and LDC, T_{DIP} profiles were determined at day 5 (bold lines). Horizontal bar in a (WMA) and b (EMA) delineates the mean phosphacline depth (mean ± sd: 20 ± 7 m, and 44 ± 10 m, respectively) as determined by Moutin et al. (2018). At WGY (c), DIP concentrations were > 100 nM at all depths.

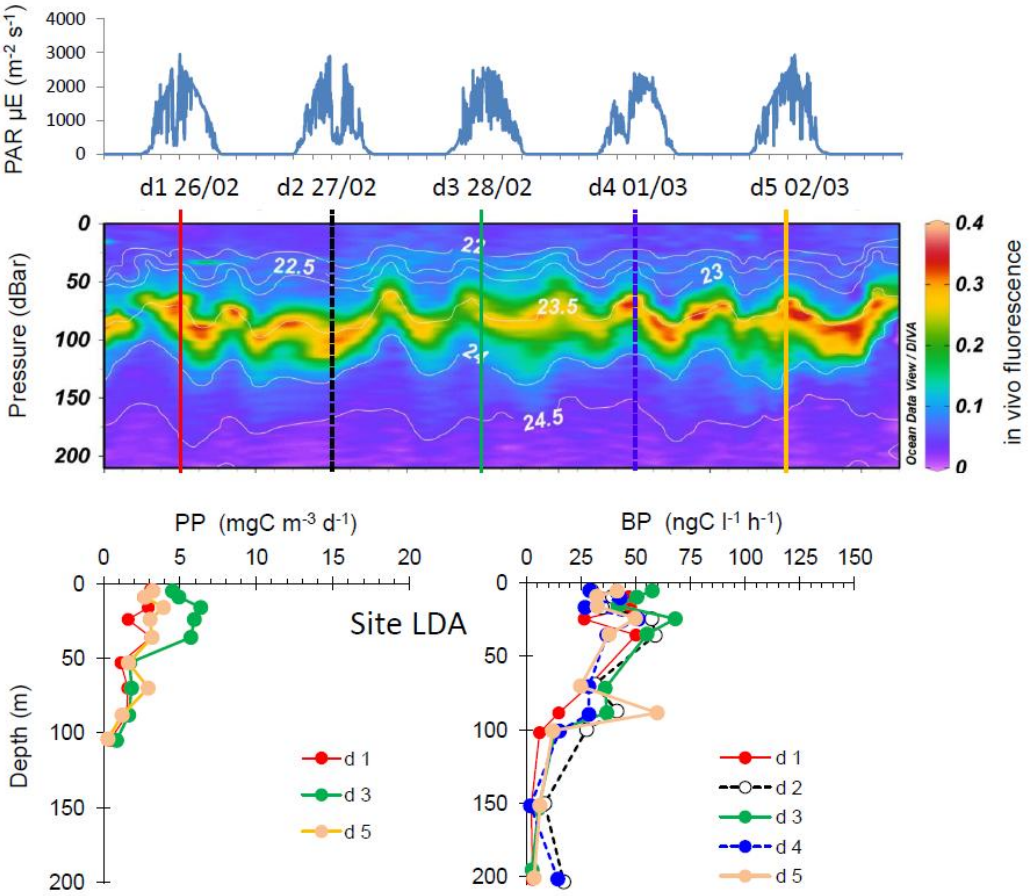


Figure 5 Evolution of surface PAR, in vivo fluorescence, PP and BP at the site LDA. Time units in local time, day1 was February 26, 2015. BP samples were taken at the 12:00 PM ctd cast, while samples for $PP_{in\ situ}$ were taken at the 3:00 AM ctd casts (day 1, 3 and 5). On the in vivo fluorescence graph, vertical bars show the 12:00 AM ctd cast sampled for BP each day (1 to 5) with corresponding colours used for plotting BP vertical profiles.

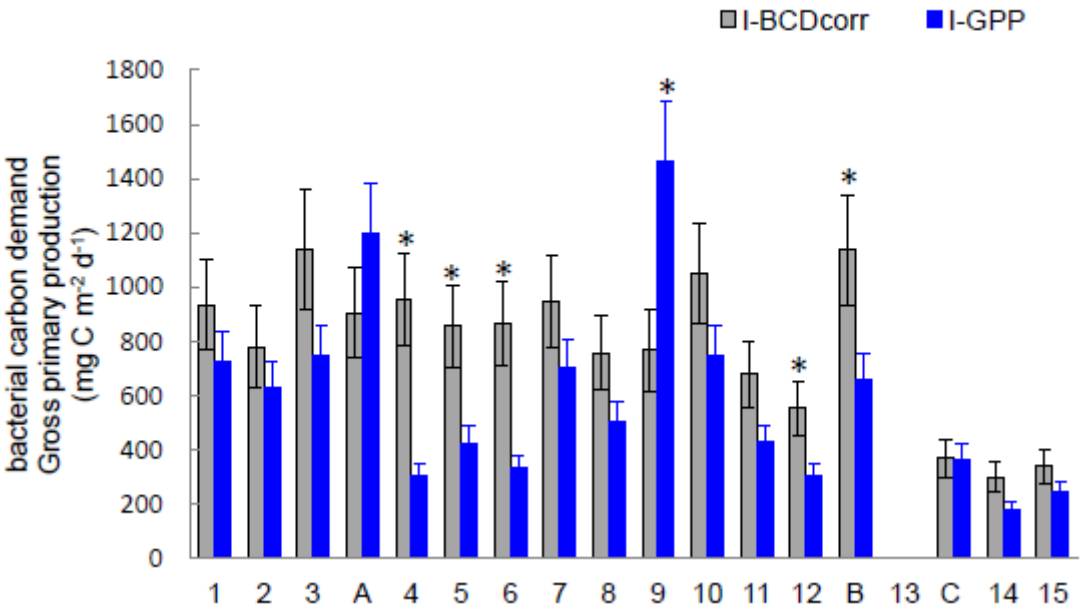


Figure 10 Distribution of integrated bacterial carbon demand corrected for *Prochlorococcus* assimilation) and based on a 8% BGE ($I\text{-}BCD_{corr,}$ grey bars), gross primary production derived from IPP_{deck} (I-GPP, blue bars) along the transect. Error bars are standard errors, calculated using propagation of errors.* indicates stations where the hypothesis Ho that the 95% confidence interval of the difference (I-BCD minus I-GPP) includes zero was rejected.

Response to Anonymous Referee #2

In this article the authors present the results from a study into bacterial and primary production in the tropical south Pacific ocean. The paper fits perfectly within the scope of Biogeosciences. I found the article interesting to read with some very interesting insights into the carbon balance of this part of the Tropical South Pacific, a region that has been rather less studied than some of the other oceanic provinces.
While the actual methods used can be considered as relatively classic in the domain, their application to this little studied area is novel. Indeed, although several authors have worked in the Tropical South Pacific, the vast majority of these studies have looked at either N2 fixation alone or have been conducted in the coastal areas near to Islands.
This data from the open ocean is particularly interesting and novel. The assumptions of the methods are appropriate and are clearly outlines.

I am wondering why was the ratio 400ml of bacterial 'inoculum' chosen for addition to 2.6L?
It was a typo error that we have corrected. We added 400 ml in a volume of 1.6 L so that the dilution factor was 20%. In oligotrophic environments, adding only 10% usually leads to a very long lag phase.

The conclusions are appropriate and provide some interesting insights into what is limiting bacterial production in this part of the ocean. Notably, it appears that available N is the limiting factor - which of course underlines the importance of N2 fixing organisms in this environment, as has been already shown by other work from this group.

I was a little perplexed as to why some results were shown in the methods section Pg 4, line 135.
In the M&M section, we wanted to justify why we used in vivo fluorescence only to describe shape of vertical profiles, depths of dcm, high frequency time evolution, whereas discrete measures of chlorophyll by fluorometry were used to estimate and compare chlorophyll biomass stocks. This is why we prefer to keep this information in the M&M. However, it does not need to be developed to a great extent, and the last paragraph was reduced as follows:
'Due to the heterogeneity at the time of sampling and the nature of the populations present, i.e. essentially different fluorescence yields over depth and species (Neveux et al., 2010), the overall correlation of in vivo fluorescence (chl iv) with chl a was very patchy (chl a=1.582 * chl iv + 0.0241, n = 169, r = 0.61). Thus in vivo fluorescence was used to track high frequency variability at the LD sites, the shape of vertical profile's distributions and the location of the dcm, as well as longitudinal trends. But fluorometric discrete data (chl a) was always used when calculating and comparing integrated stocks.'

The results section is sufficient to support the conclusions - I have one comment here though - it was a little awkward to have quite a few associated datasets were in other articles - it was a bit difficult to do a "stand-alone" review. But the authors do clearly give credit for other work and they clearly indicate what their new additions are.
This is inevitably a problem during the process of special issues. Among the 6 publications not published in December 2017, 3 of them are now submitted in Biogeosciences Discussions and one in press has been published:
Bonnet, S., Caffin M., Berthelot H., Grosso, O., Benavides, M., Helias-Nuninge, H., Guieu, C., Stenegren, M. and Foster, R.: In depth characterization of diazotroph activity across the

Western Tropical South Pacific hot spot of N_2 fixation, Biogeosciences Discuss., doi.org/10.5194/bg-2017-567, 2018
Dupouy, C., Frouin, R., Tedetti, M , Maillard, M.., Rodier, M., Lombard, F., Guidi, L., Picheral, M., Duhamel, S., Charrière, B., and Sempéré, R.: diazotrophic *Trichodesmium* influences ocean color and pigment composition in the South West tropical Pacific, Biogeosciences Discuss., doi.org/10.5194/bg-2017-570, in review, 2018
Moutin, T., Wagener, T., Caffin, M., Fumenia, A., Gimenez, A., Baklouti, M., Bouruet-Aubertot, P., Pujo-Pay, M., Leblanc, K., Lefevre, M., Helias Nunige, S., Leblond, N., Grosso, O. and de Verneil, A.: Nutrient availability and the ultimate control of the biological carbon pump in the Western Tropical South Pacific Ocean. Biogeosciences Discuss., /doi.org/10.5194/bg-2017-565, 2018.
Tenorio, M., Dupouy C., Rodier, M., and Neveux, J. Filamentous cyanobacteria and picoplankton in the South Western Tropical Pacific Ocean (Loyalty Channel, Melanesian Archipelago) during an El Nino episode, Appl. Microb. Ecol., doi.org/10.3354/ame01873, 2018

The experiments and calculations are well described and will allow for replication by other scientists.
The Title clearly reflects the contents, particularly if we take into account the whole group of papers from the Outpace experiment.
The abstract is clear but I wondering if the last sentence should not appear earlier in the text, it does seem to be a little be disconnected from the rest of the text. Perhaps the authors can rephrase it if they wish to leave it as a last sentence or move it up.
This sentence was moved upwards in the abstract

Yes, the article is well structured, clear and I really enjoyed reading it. The language is fluent and clear and the appropriate formulae and correction factors used are presented clearly when needed.

Concerning the tables: Table 1 and 2 : both of these tables are a little blurry – maybe check that in a revised version?
It is because we had to paste an image in an A4 format whereas the initial table was in a Landscape format, not accepted in the edited version. We will work with the editor to make sure that our tables appear clearly in the final version of the manuscript. Dealing with the content of Table 1, we also organized referenced areas in a more logical order, roughly from west to east.

Also, can the authors add the units into the table (I know they are in the legend, but I always find it easier to follow when they are in the table itself).
It is done

Table 5 : can the authors add in if its the mean +/- the SD or the SE?
It is ± SE. It was added on the Table 5

Figure 1 : is a little hard to see - but maybe it's my printout - nevertheless, can the authors check that the figure is clear and not blurry.
In the original ppt version, figures are not blurry. In addition, we made a new version of figure 1 where letters are better contrasted and the different groups of stations (WMA, EMA and WGY) are indicated. See the new Figure 1 at this end of the responses to the reviewer's comments

Figure 3 : check the format of the legend titles (add in uppercase letters when needed).
This has been corrected

Figure 4: why did the authors choose to put in the black dotted lines? It rather draws the eye at the cost of the other profiles.
We made a new Fig.4 (please see at the end of the responses to the reviewer's comments)

Overall, can the authors unify the format of the axis titles on the figures - some have () some do not. Also can they check the clarity of the contour maps and the colour of the words/numbers on the graphics - sometimes they are hard to read (see figs. 5-7b).
Parenthesis for units have been added everywhere. In their original version in ppt format, the Figures are not blurry We will take care of that during editing process of the revised version

pg 9 line 341 : non signficant for PP
This has been corrected

line 250 : what do the authors mean here 'determined by fluorometry'? Don't both methods employ fluorometrey (Turner vs CTD)?
Yes, you are right. The term 'determined by fluorometry' was removed

pg 11, line 420 : 6-12% is not that low.
We removed the term 'low'

line 440 : check spelling of Lemee here (it's okin the Refs).
This has been corrected

Paragraph starting 455: negative NCP values have also been observed in the oligotrophic water off-shore of New Caledonia (Pringault et al. Biogeosciences 2007).
Yes, this reference was added in the ms.

I agree with the authors that calculating up hourly incubation values to daily ones is fraught with errors. Do the authors have an estimate of how much error may be introduced from these factors?
Diel variability of BP was studied in the eastern south Pacific gyre at three sites: in the open sea away from Marquesas Islands, in the center of the South Pacific gyre, and in the eastern part of the south Pacific gyre (Van Wambeke et al., 2008). At these sites, a Lagrangian sampling strategy was used and we followed BP every 3 h up to 72 h long. From this study, the coefficients of variation (SD/Mean ratio) of euphotic zone-integrated hourly BP were 13, 16 and 19%. With the number of profiles varying between 9 and 16 per site, the standard error (SE represented on average 5 % of the mean. We used this value in the context of the OUTPACE cruise to estimate the SE introduced by the conversion from hourly to daily bacterial carbon demand, using propagation of errors (SE. related to triplicate variability of BP, and SE related to daily variability). The corresponding SE is now plotted in Fig. 3a. We also added this information in the text.

It is interesting to note that Prochlorococcus could be responsible for up to 56% of leucine uptake - this could have some very strong implications for BCD calculations and hence, ecosystem metabolism calculations in areas where Prochlorococcus is abundant.
What about the diazotrophs? Do they take up leucine? Is there any information on this?

Yes, co-author S. Duhamel did some cell sorting of *Crocosphera*-like cells which peaked at 60 m at the site LDC. She detected significant uptake of leucine by these cells in light and dark conditions. Although the activity was significantly detected per cell, due to their low abundance, their participation to the bulk uptake of leucine was very low. These results will be presented in a manuscript in preparation outside of this Special Issue. Moreover, assimilation of dissolved organic nitrogen labeled with ^{15}N and observed by Nanosims technique also suggested assimilation by *Trichodesmium*, although the hypothesis that this labeling could be obtained indirectly after a transfer via epibiontic heterotrophic bacteria could not be ruled out (Benavides et al., 2017).

530 : what is an artificial diazotroph culture?
We wanted to insist on the fact that the information did not concern natural environment. Of course a culture is not e natural environment. We removed the term 'artificial'

570: not sure what the authors mean here in the sentence starting "They also showed..." - can the authors revised this?
The sentence was modified as:
'They also showed a highly dynamic *Crocosphaer*a growth and decay during diel cycles survey, suggesting rapid switch between cell growth and mortality processes, such as grazing and viral infection.'

589: what do the authors mean by "highly diverse metabolic status" - maybe clarify the meaning here.
This last sentence was removed

New versions of some Figures

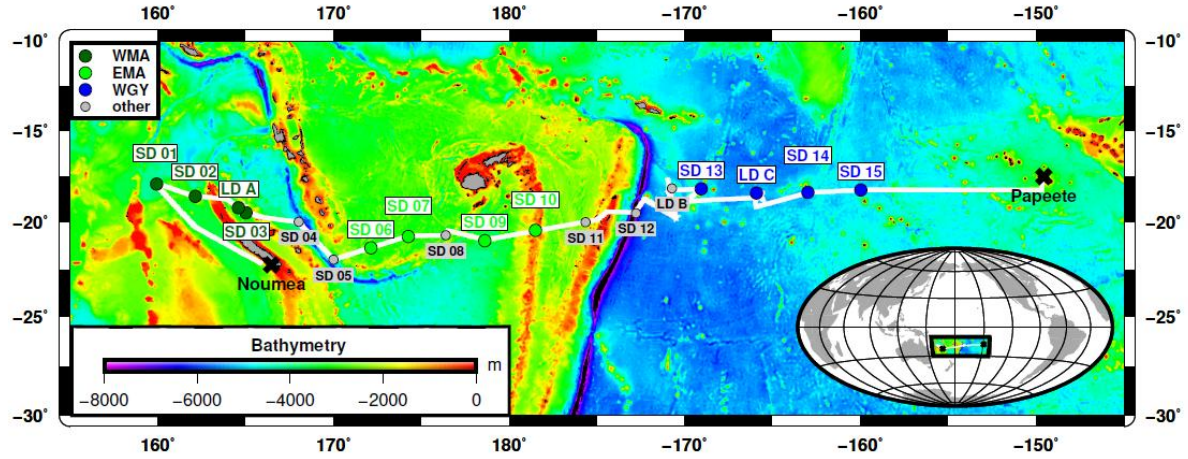


Figure 1 Stations locations during the OUTPACE cruise. The white line shows the ship track (data from the hull-mounted ADCP positioning system). In dark green WMA (western Melanesian Archipelago) included SD1, 2, 3 and LDA; in light green, EMA: eastern Melanesian Archipelago included SD 6, 7, 9 and 10 and in blue WGY (western gyre) included stations SD13, 14, 15 and LDC. Figure courtesy of T Wagener.

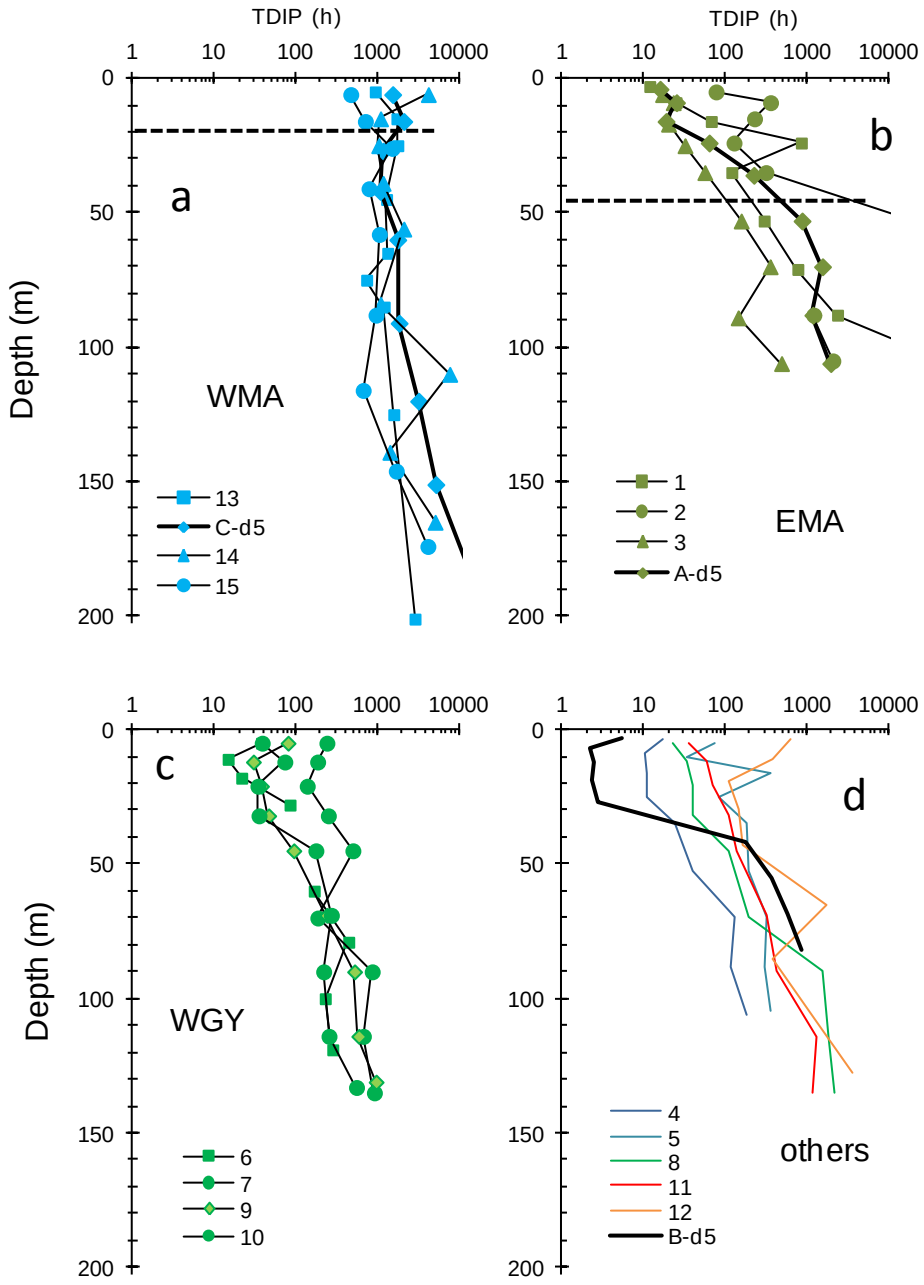


Figure 4 Vertical distributions of phosphate turnover times (T_{DIP}) in groups of stations WMA (a), EMA (b), WGY (c) and other stations (d). At the long-duration stations LDA, LDB and LDC, T_{DIP} profiles were determined at day 5 (bold lines). Horizontal bar in a (WMA) and b (EMA) delineates the mean phosphacline depth (mean ± SD: 20 ± 7 m, and 44 ± 10 m, respectively) as determined by Moutin et al. (2018). At WGY (c), DIP concentrations were > 100 nM at all depths.

Erratum in AC1 and AC2 about Fig. 4

We apologize for that, but an error occurred when presenting the new Figure 4 in our author comments AC1 and AC2. The codes of stations were correct, the color codes were correct, and consequently 4a (blue) is WGY and not WMA, 4b (dark green) is WMA, and not EMA, and 4c (light green) is EMA, but not WGY. The mean phosphacline depths of EMA and WMA group of stations have been moved accordingly.

Note also that we were informed by an e-mail dated on March 17, 2018 that the ms by Duhamel et al 'Mixotrophic metabolism by natural communities of unicellular cyanobacteria in the western tropical South Pacific Ocean' has been accepted for publication in 'Environmental Microbiology'. It seems to us that this information is relevant as a part of the discussion on our ms discuss the bias related to assimilation of leucine by *Prochlorococcus*.

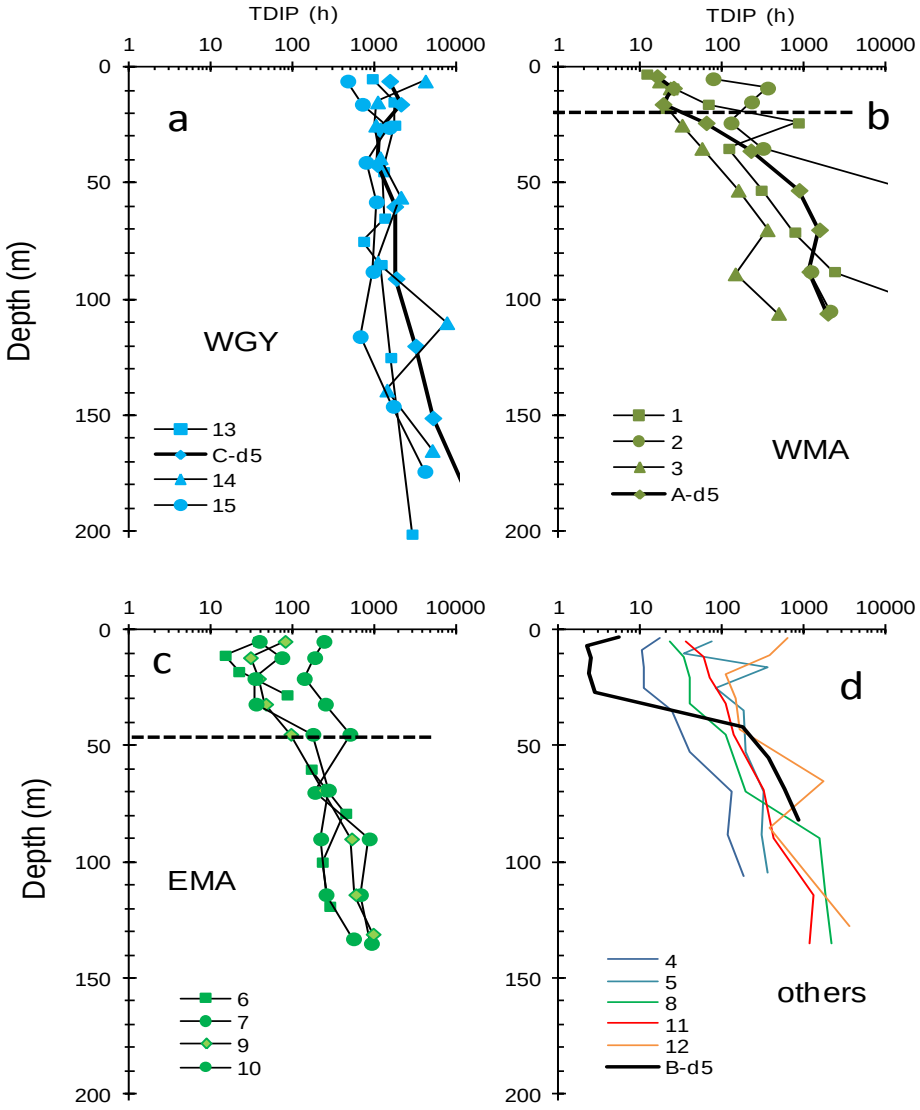


Figure 4 Vertical distributions of phosphate turnover times (T_{DIP}) in groups of stations WGY (a), WMA (b), EMA (c) and other stations (d). At the long-duration stations LDA, LDB and LDC, T_{DIP} profiles were determined at day 5 (bold lines). Horizontal bar in b (WMA) and c (EMA) delineates the mean phosphacline depth (mean ± SD: 20 ± 7 m, and 44 ± 10 m,

respectively) as determined by Moutin et al. (2018). At WGY (a), DIP concentrations were > 100 nM at all depths.